Received: 27 June 2022 | Accepted: 13 June 2023

DOI: 10.1111/1365-2435.14479

Functional Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Lipid biomarkers reveal trophic relationships and energetic trade-offs in contrasting phenotypes of the cold-water coral *Desmophyllum dianthus* in Comau Fjord, Chile

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Funding information
Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Grant/Award Number: Strategy Fund DACCOR #IP74010002; Bundesministerium für Bildung und Forschung, Grant/Award Number: PACOC/CONICYT-BMBF: 20140041 and 01DN15024

Handling Editor: Scott Burgess

Abstract

1. Benthic suspension feeders like corals and sponges are important bioengineers in many marine habitats, from the shallow tropics to the depth of polar oceans. While they are generally considered opportunistic, little is known about their actual in situ diet. To tackle this limitation, fatty acid trophic markers (FATMs) have been employed to gain insights into the composition of their diet. Yet, these in situ studies have not been combined with physiological investigations to understand how physiological limitations may modulate the biochemistry of these organisms.
2. Here, we used the cold-water coral (CWC) *Desmophyllum dianthus* in its natural habitat in Comau Fjord (Northern Patagonia, Chile) as our model species to assess the trophic ecology in response to contrasting physico-chemical conditions (variable vs. stable) and ecological drivers (food availability) at three shallow sites and one deep site. We took advantage of the expression of two distinct phenotypes with contrasting performance (growth, biomass, respiration) coinciding with the differences in sampling depth. We analysed the corals' fatty acid composition to evaluate the utility of FATM profiles to gain dietary insights and assess how performance trade-offs potentially modulate an organism's FATM composition.
3. We found that 20:1(n-9) zooplankton markers dominated the deep high-performance phenotype, while 20:5(n-3) and 22:6(n-3) diatom and flagellate markers, respectively, are more prominent in shallow low-performance phenotype. Surprisingly, both energy stores and performance were higher in the deep phenotype, in spite of measured lower zooplankton availability.
4. Essential FA concentrations were conserved across sites, likely reflecting required levels for coral functioning and survival. While the deep high-performance

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phenotype met with these requirements, the low-performance phenotype appeared to need more energy to maintain functionality in its highly variable environment, potentially causing intrinsic re-allocations of energy and enrichment in certain essential markers (20:5(n-3), 22:6(n-3)).
5. Our analysis highlights the biological and ecological insights that can be gained from FATM profiles in CWCs, but also cautions the reliability of FATM as diet tracers under limiting environmental conditions that may also be applicable to other marine organisms.

KEYWORDS
cold-water corals, essential fatty acids, fatty acids trophic markers, health indicators, physiological requirements, trophic ecology

1 | INTRODUCTION

Benthic suspension feeders from shallow tropics to polar deep sea include the most important bioengineer species in the ocean (Gili & Coma, 1998; Roberts et al., 2006; Rossi et al., 2017). Particularly, corals and sponges create complex habitats that are able to sustain a high biodiversity (Maldonado et al., 2015; Rogers, 1999), including many commercially important fish species (Buhl-Mortensen & Mortensen, 2004; Fosså et al., 2002; Roberts et al., 2006). These biodiversity hotspots are of considerable ecological and economic value (Foley et al., 2010) and considered vulnerable marine ecosystems under pressure that need better protection. This requires a better understanding of their baseline conditions to project their fate under future conditions.

While most tropical corals are mixotrophic due to their symbiosis with Symbiodiniacea algae in shallow water, the deep-dwelling and higher latitude cold-water corals (CWCs) are exclusively heterotrophic. The availability of food (both in quantity and quality), however, affects an organism's physiological performance, like their metabolic rate and growth, as has been observed in CWCs (Larsson et al., 2013; Maier et al., 2021; Naumann et al., 2011). Performance is expected to be affected by altered environmental parameters (Sweetman et al., 2017), however, it was shown that higher food availability may fuel resilience to deteriorating environmental conditions and can compensate otherwise limiting conditions (e.g. Büscher et al., 2017; Georgian et al., 2016; Maier et al., 2016; Martínez-Alarcón et al., 2019).

Benthic deep-sea communities like CWCs may be tolerant and resilient to projected future changes in temperature and aragonite saturation state as long as single abiotic stressors are considered (e.g. Büscher et al., 2017; Dorey et al., 2020; Hennige et al., 2015; but see also e.g. Georgian et al., 2016; Gori et al., 2016; Maier et al., 2009). However, combined changes in physico-chemical conditions and food availability (multiple stressors) have been shown to compromise performance in CWCs (Büscher et al., 2019; Hennige et al., 2015) and other foundation species (Ingels et al., 2012). Similar to other benthic suspension-feeding omnivores, CWCs gain their metabolic energy strictly from heterotrophic feeding on a variety of food particles ranging from microbes to phyto- and zooplankton (Duineveld et al., 2004; Höfer et al., 2018; Maier et al., 2019; Mueller et al., 2014; Rakka et al., 2021), where the zooplankton appears to provide a key energy source to sustain their metabolic needs (Maier et al., 2019, 2020, 2021; Naumann et al., 2011). Thus, the relative availability of food along the in situ plankton size spectrum may be crucial to determine the coral adaptation capability to future environmental conditions. However, still little is known about the feeding ecology of foundation species like CWCs and the role of food on sustaining in situ fitness as well as physiological performance.

The analysis of energy reserves and especially the lipid/fatty acid (FA) composition of organisms can give important insights into their natural diet. Lipids are key components of an organism's biomass and their fatty acids are promising biochemical markers providing insights into the nutritional status, ecology and health of organisms (Dalsgaard et al., 2003; Imbs & Yakovleva, 2012; Kim et al., 2021; Rocker et al., 2019). In general, lipids provide more metabolic energy per gram than any other tissue compound like proteins or carbohydrates (Bureau et al., 2002) and represent a diverse group of large biological molecules (Imbs et al., 2019; Joseph, 1979). Dietary lipids are required by animals for the provision of metabolic energy, generated as ATP through the oxidative metabolism of fatty acids, and for the production of polar lipids, that is, phospholipids and sphingolipids, necessary for the formation of cell membranes. This dual role is reflected in the compartmentalization of body lipids into adipose tissue, composed mainly of wax esters and/or triacylglycerols, and cell membrane lipids composed mainly of polar lipids and cholesterol (Sargent et al., 1993). Their balance is critical for the organisms as they are involved in the majority of biochemical and physiological processes in organisms (Russo, 2009; Tocher, 2003) and also linked to their stress resistance (Imbs & Yakovleva, 2012; Yamashiro et al., 2005).

The analysis of FA and fatty alcohols (FAlcs) composition—so called fatty acid trophic markers (FATM)—has been widely used to trace the main food sources in marine organisms (e.g. Budge et al., 2006; Dalsgaard et al., 2003; Graeve et al., 1997). Similarly, specific fatty acid ratios (e.g. DHA/EPA, n-3 PUFA/n-6 PUFA) serve as useful tracers of nutritional conditions (Budge et al., 2006; Dalsgaard et al., 2003; Graeve et al., 1997). At the same time, many

polyunsaturated fatty acids (PUFAs) are essential for an organism's functioning and health and their biosynthetic pathways together with the organism's ability to modify FATM marker signals should be considered as this can modify the pure dietary FATM signal (Galloway & Budge, 2020; Kim et al., 2021; Rocker et al., 2019). Biosynthetic pathways are clearly described for phyto- and zooplankton and these pathways underscore their FATM profiles as well as their ability of trophic upgrading (i.e. the modification of essential dietary precursor PUFAs like 18:3(n-3) (ALA—alpha linolenic acid) to essential LC PUFAs like EPA; a schematic biosynthesis pathway is depicted in Supporting Information Figure S1). De novo synthesis of long-chain PUFAs, however, is linked to the unique possession of specific desaturase enzymes (Δ12, Δ15 Kabeya et al., 2020). These are key enzymes in primary producers that synthesize LC PUFA precursors, but these enzymes are lacking in higher trophic levels, for example, fishes. Recently, evidences show that intermediate consumers and invertebrate groups, including tropical corals, do also possess such enzymes (Kabeya et al., 2018; Monroig & Kabeya, 2018). This needs to be considered in future FATM studies.

In CWCs, FATM analyses, together with the study of the corals' isotopic composition, may identify the corals in situ main food sources, distinguishing between phytoplankton- (Duineveld et al., 2004, 2012; Kiriakoulakis et al., 2005) and zooplankton-dominated diets (Carlier et al., 2009; Dodds et al., 2009; Kiriakoulakis et al., 2005) at low and high supply levels (Dodds et al., 2009; Gori et al., 2018). Thus, biomarkers can provide a powerful tool to identify potential differences in prey composition. Since corals are considered omnivorous (Carlier et al., 2009; Duineveld et al., 2004; Höfer et al., 2018), unselective regarding their prey and consume what is provided (Höfer et al., 2018), CWCs represent an ideal system to infer nutritional condition and trophic ecology from their FATM profiles (Dodds et al., 2009; Duineveld et al., 2012; Gori et al., 2018; Naumann et al., 2015). However, these data should be carefully considered since physiological responses to unfavourable conditions (e.g. like eutrophication in tropical corals Kim et al., 2021; Rocker et al., 2019) may affect the trophic transfer or modification of biomarkers and potentially distort the diet signal (Galloway & Budge, 2020). While first studies with tropical corals addressed the potential changes in biosynthetic pathways under optimal and suboptimal conditions and identified putative FA indicators for coral health (Kim et al., 2021; Rocker et al., 2019), similar investigations for CWCs are still missing.

Here we investigated the suitability of biomarkers to assess dietary composition and health status in opportunistic suspension-feeding CWCs from contrasting habitats, using *Desmophyllum dianthus* in its natural Comau Fjord environment as our model species. We analysed the FATM profile in *D. dianthus* individuals sampled along strong environmental gradients (both horizontal and vertical), and analysed the results against the background of concomitant data on coral physiology (and distinct coral phenotypes, Beck et al., 2022) and zooplankton composition (Garcia-Herrera et al., 2022). This allowed us to assess the relationship between the FATM signal and the available diet, as well as possible shifts due to coral physiology influencing the FATM composition. Ultimately, the knowledge of how contrasting phenotypes modulate their lipid composition provides insights into potentially inherent physiological constraints on FA biosynthesis pathways in CWCs and other heterotrophic organisms, and an important step forward to advance this line of research in deep-sea foundation species.

2 | MATERIALS AND METHODS

2.1 | Site and collection

The study was conducted in Comau Fjord, Northern Patagonia, Chile (Figure 1), one of the few places worldwide where CWCs emerged from the deep and inhabited shallow waters (Häussermann et al., 2021). Local populations of *D. dianthus* within this region are found in very contrasting environments, including both deep and shallow waters, as well as head and mouth of the fjord (Beck et al., 2022). To represent the horizontal and vertical environmental gradients, corals were collected at 20 m depth at three stations (A,E,F) along the main fjord axis, and at two depths (20 and 280–290 m) at station (E), midway along the horizontal transect. At each sampling location, six *D. dianthus* individuals were collected in September 2016 (6–22 September) by SCUBA divers (shallow sites) and an ROV (deep site, Commander 2, Mariscope Ingeniería, Puerto Montt, Chile; modified with manipulator arms and high-resolution camera). The collection of deep-water specimens required the ROV to be equipped with a wire frame and a water-tight bag attached to scrape the corals from the wall. The detached corals were secured in the bag, sealed and brought to the surface avoiding sample contact with the brackish surface layer. We identified two different phenotypes that differed in physiological performance (growth, biomass and respiration) coinciding with (but not necessarily causally related to) differences with sampling depth.

2.2 | Environmental and physiological background data

The physico-chemical environmental conditions during the sampling period were characterized along the entire fjord by CTD vertical profiles ranging from the surface down to the seafloor. These CTD casts were conducted between 7 and 12 September 2016 at a total of seven stations in the centre of the Fjord (Figure 1, yellow triangles). The CTD (SBE 19plus V2 SeaCAT profiler CTD, Sea-Bird Scientific, USA) was equipped with oxygen (SBE 43 dissolved oxygen, Sea-Bird Scientific, USA) and pH sensors (SBE 18 pH, Sea-Bird Scientific, USA).

The coral performance (i.e. biomass, respiration and growth) was assessed subsequently to the coral sampling in a separate year-long in situ experiment. Corals were collected at the four sites, prepared for re-installation and re-collected seasonally after 4, 8 and 11 month to assess their performance. In brief, growth was measured through the buoyant weight technique (Jokiel et al., 1978) and respiration through closed-cell incubations of 6-h duration. Furthermore,

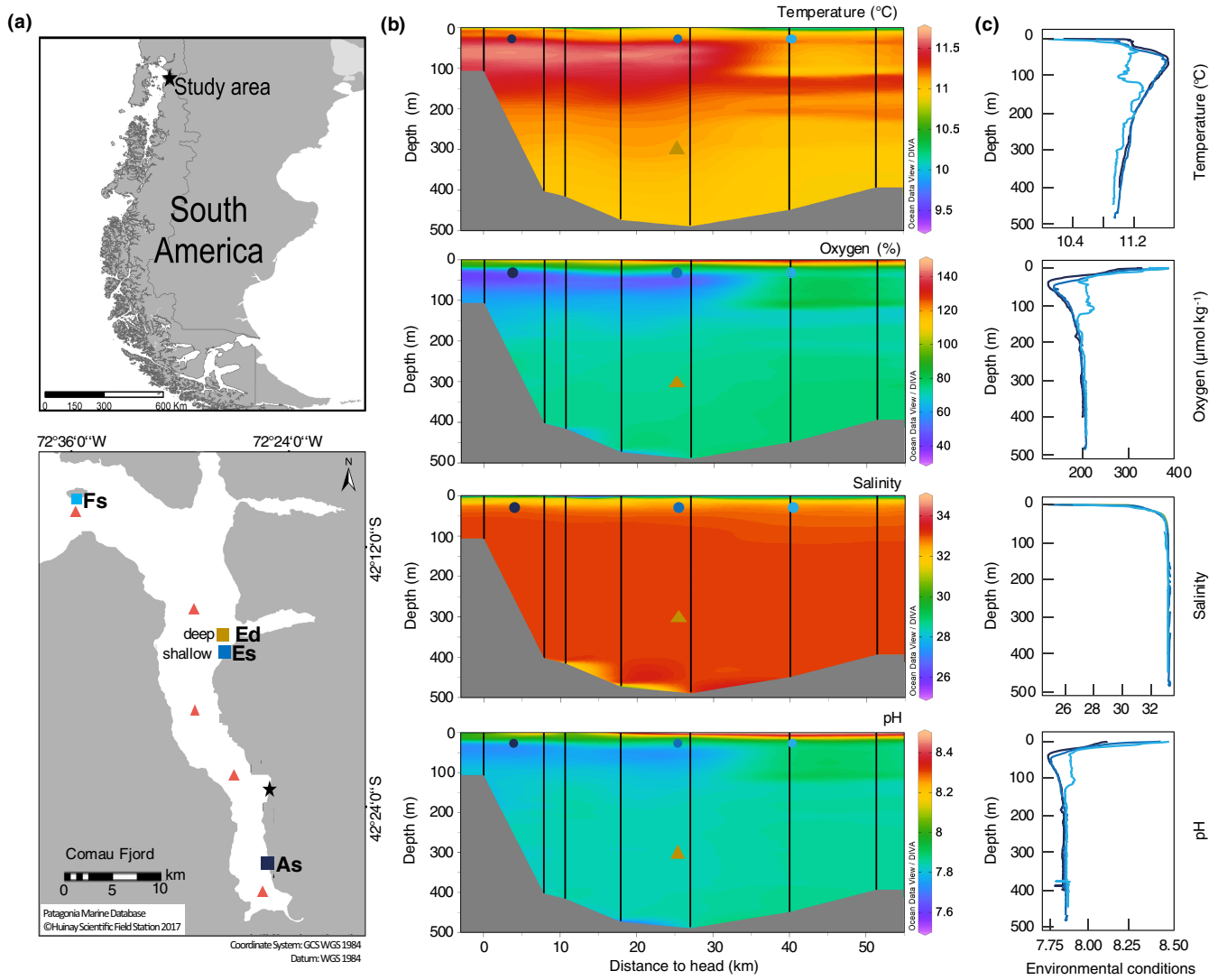

FIGURE 1 Sample sites and physico-chemical conditions in Comau Fjord, Chile. (a) Study area is located in South America (upper panel) in Fjord Comau in Northern Patagonia, Chile (lower panel). Shallow (20 m) coral sampling sites are denoted with light to dark blue squares (stations As, Es, Fs), the deep site (280–290 m, Ed) is denoted in dark yellow. Oceanographic stations along the fjord are marked with red triangles. (b) Cross sections of temperature (°C), oxygen saturation (%), salinity and pH from fjord head to mouth and deep to shallow are provided. Sampling stations (triangles in (a)) are shown by vertical black lines and position of sampling sites is indicated by circles and triangles. (c) Vertical profiles of temperature, oxygen saturation, salinity and pH at the sampling stations (A,E,F) are shown. Line colours correspond to the blue colour hues in (a).

separate corals were prepared and collected at the same seasonal time scales, snap frozen and the corals tissue biomass determined. The procedure and seasonally resolved responses are presented in Beck et al. (2022). Here, we provide the average performance over all seasons to obtain a site-specific representation of coral performance and phenotype. In addition, scaled side-view photographs of freshly collected corals were taken in September 2016 to document differences in coral appearance between sites.

2.3 | Coral sample processing and FATM analysis

After collection, corals were transported to the Huinay field station and maintained in a flow-through aquaria system for 3–14 days, due to logistical reasons (intense field and laboratory work of parallel studies as published in Beck et al., 2022; Garcia-Herrera et al., 2022). Recently analysed changes in the FATM composition of corals after transplantation to different sites in situ showed that changes in FATM of distinct phenotypes are rather slow and their FATM signal did not fully converge after being 3 months at the same in situ location (K. Beck work in progress). We thus do not expect a measurable effect after only 3–14 days under laboratory conditions in natural seawater. We thus do not expect a measurable effect after only 3–14 days under laboratory conditions in natural seawater. Corals were then snap frozen in liquid nitrogen and maintained at −80°C until further processing. In the laboratory corals were crushed and ground to a relatively fine and homogeneous powder in a liquid nitrogen cooled stainless steel mortar. Subsequently, the

total ground material was weighed (ranging 970–8250 mg per coral individual) and subsampled for downstream analyses (i.e. ash free dry weight (AFDW) determination and fatty acid analysis) as follows: Approximately 300 mg per sample were used to determine ash free dry weight (~10% of the whole sample) and a minimum of 700 mg per sample (700–6600 mg, approx. 80% of the whole animal) for lipid concentration and fatty acid composition analyses. The remaining material (~10%) was snap frozen and returned to −80°C. Ash free dry weight was determined by transferring the subsample to a pre-combusted aluminium weighing pan and dried to constant dry weight for approx. 24 h in an oven at 60°C. Subsequently, the sample was weighed and combusted at 450°C for 6 h. Ash free dry weight was used to normalize the quantitative lipid and fatty acid composition analyses by extrapolating measurement to the total crushed coral sample and standardized to the organic fraction of the samples. Note that processing involved grinding the whole animal including the endolith-infested skeleton that may contribute to the phytoplankton signal (more information see Supporting Information Appendix S1). However, we expect a minor influence as the coral biomass outweighs the biomass of coral-associated endoliths by an order of magnitude (e.g. Schlichter et al., 1995), thus diluting the signal. More importantly, the translocation of endolith photosynthates in darkness is an order of magnitude lower than in light-exposed shallow water tropical corals (Schlichter et al., 1995). We thus expect the contribution to be insignificant in the dim light of our study.

The lipid subsample was freeze-dried for approx. 24 h (at −55°C, 1 mbar, Alpha 1–4 LSC basic, Martin Christ Gefriertrocknungsanalgen GmbH) and total lipid extracted in dichloromethan:methanol (DCM:MeOH, 2:1 per volume), modified after Folch et al. (1957), using dichlormethan instead of chloroform with methanol 2:1. Aqueous KCl solution was added prior to centrifugation for phase separation. The extracted total lipid mass was determined gravimetrically and expressed as normalized to AFDW. As an internal standard, tricosanoic acid methyl ester (23:0) was added to each sample (1 $\mu g\,\mu L^{-1}$ in n-Hexan). Transesterification of the lipid extracts was performed with 3% sulphuric acid in methanol for 4 h at 80°C under nitrogen atmosphere. After adding 4 mL of water, the FAMEs were extracted three times with 2 mL n-Hexan, dried with nitrogen and redissolved for the measurements in n-Hexan. A gas chromatograph with Flame Ionization Detector (HP 6890N, Agilent Technologies, Inc) DB-FFAP column (Agilent, lenght 30 m × inner diameter 0.25 mm × film thickness 25 µm) was used to determine the fatty acid methyl esters and fatty alcohols (Graeve et al., 1997; Kattner & Fricke, 1986). Individual fatty acids (FAs) and fatty alcohol compounds (FAlc) were identified by their retention time and compared to known standards. Unknown peaks with less than one percentage contribution were excluded and the remaining chromatograms were evaluated using the Clarity Chromatography Software (version 8.6) from DataApex. Total lipid mass per individual was derived by GC-FA/FAlc content from the measurements. Individual FA and FAlc compounds were calculated as relative percentage based on the total FA or FAlc concentration and also normalized to AFDW.

2.4 | Data analyses and statistics

Analyses were performed using R-Studio 1.3.1073 with R version 4.0.2 (R Core Team, 2020; RStudio Team, 2020). Site-specific differences in both FA and FAlc percentage composition were visualized using heatmaps with hierarchical clustering of both samples and FA/FAlc (package ComplexHeatmap, v2.6.2, Gu et al., 2016) and characterized by ordination analyses based on weighted log-ratio analysis (LRA) using the package 'easyCODA' (Greenacre, 2018). LRAs were performed on the total FA as well as total FAlc marker sets. Within LRA biplots loading vectors were limited to the major contributing markers following the procedure described in 'easyCODA' (Greenacre, 2018) or Graeve & Greenacre (2020). Here we also summed markers for bacteria-specific origin: i15:0, ai15:0, i17:0 and 18:1(n-7) (Boschker & Middelburg, 2002; Brett et al., 2006; Meziane & Tsuchiya, 2000) to identify their contribution to CWC diet. In addition, the sum of FA and FAlc groups (SFA—saturated fatty acids/alcohols, MUFA—monounsaturated fatty acids/alcohols and PUFA) were derived as both relative and absolute concentration and ratios of putative FA trophic marker (e.g. 18:1(n-9)/18:1(n-7)), DHA/EPA, sum of long-chain MUFA (e.g. 20:1(n-9), 20:1(n-7)) and the ratio of photosynthetic ¥(sum of 16:1(n-7) and 18:1(n-7)) versus animal-derived input (sum of 18:1(n-9), 20:1(n-9) and 22:1(n-11)) (Dalsgaard et al., 2003; Graeve et al., 1997; Radice et al., 2019; Sargent & Whittle, 1981) as well as putative health indicators (e.g. EPA/ARA, PUFAn3/PUFAn6, Kim et al., 2021; Rocker et al., 2019) were calculated from the FATM signal. One-factorial ANOVA (normal and equal variance), Welch one-way test (violation of homoscedasticity) or Kruskal–Wallis (violation of both homoscedasticity and normality) test were performed on total lipid composition, FA or Falc classes, important dietary compounds/ratios (i.e. 20:1(n-9), trophic marker ratio: 18:1(n-9) / 18:1(n-7)) as well as essential Fas or health markers (e.g. EPA, DPA) to identify site-specific differences. Pairwise tests were used (with Tukey or Bonferroni correction) to reveal post hoc differences between individual sites. Fatty acid class composition differences among sites were tested with PERMANOVA in the R package 'vegan'.

CTD data were plotted using Ocean Data View (Schlitzer, 2021). In the along-fjord profiles (Figure 1b), the colour scales were adapted to highlight the structure of the entire water column. Site-specific profiles were derived from the CTD profiles closest to each station and depth-related average values obtained from these profiles per depth stratum (shallow: 20–30 m and deep: 280–300 m to cover the maximum diurnal range for the region).

3 | RESULTS

3.1 | Environmental background

The sampling period marks the end of austral winter, characterized by a strong temperature inversion near the surface due to atmospheric cooling (Figure 1b,c). Winter mixing of the upper water column was evident in all parameters measured, showing deep mixing (down to 120 m) of oxygen-rich and high pH surface waters in the outer

two stations, eroding the suboxic and low-pH subsurface (30–80 m) layer below the persisting pycnocline in the inner parts of the fjord, where mixing remained shallower than 30 m. Below 200 m we found uniform conditions with only weak vertical or lateral gradients.

Shallow corals thrive at the lower edge of the halocline under slightly lower salinity (32.49 ± 0.104 95%-CI) compared to deep corals (33.15 ± 0.0002 95%-CI, Supporting Information Figure S2).

3.2 | Coral phenotypes and their relative biochemical composition

Desmophyllum dianthus expressed two coral phenotypes that differed visually, metabolically as well as biochemically (Figure 2a–d): first, a stunted low-performance phenotype with partially retracted tissue and reduced physiological traits, encompassing all the individuals from all shallow sites, but no individual from the deep site; second, a well-developed high-performance phenotype with extended tissue and enhanced physiological traits, clustering all individuals from the one deep site and none of the individuals from any of the shallow sites. As we cannot rule out that the difference in phenotype is solely related to depth, we use 'deep' and 'shallow' as a purely qualitative value (not: explanatory factor). For the shallow phenotypes, we found a clear performance gradient from the fjord head towards the mouth (Figure 2b). Biochemically, shallow water corals from all sites were very similar and had almost equal proportion of SFA, MUFA and PUFA (30.04% ± 1.22, 29.50% ± 1.43, 40.33% ± 1.54 respectively), compared to the significantly different distinct deep high-performance coral phenotype with a specific fatty acid group composition (PERMANOVA df = 3, $F = 112.81$, $p < 0.001$, Figure 2c). Deep high-performance coral fatty acids were dominated by MUFA (60.75% ± 1.62) with lower but equal parts of PUFA and SFA (18.81% ± 0.99, 20.44% ± 0.71 respectively). Deep corals were characterized by a significantly higher total lipid content (fourfold increase, Welch's t-test, df = 3, $F = 4.09$, $p = 0.038$) and content of fatty alcohols (one-way ANOVA, df = 3, $F = 103.95$, $p < 0.001$, 33.8% ± 4.0 compared to 10% ± 2.8 across all shallow sites, Figure 2c,d).

3.3 | Fatty acid trophic marker composition

A total of 44 FA and 8 FAlc markers were determined with very characteristic and different compositions between the two phenotypes. The main FAs differentiating among phenotypes in the LRAs were in the first dimension (dim 1), which explained 79.1% of the observed variance and in particular involved the FAs 20:1(n-9) and 22:1(n-11), as well as essential FAs like 20:5(n-3) and 22:5(n-3) (Figure 3a). Thus, the clear distinction between phenotypes was also mirrored in the FA and FAlc composition (Supporting Information Figure S3 and Table S1) indicating pronounced dietary differences that support the two phenotypes.

The trophic marker ratio (18:1(n-9): 18:1(n-7) > 3, (Graeve & Greenacre, 2020, Figure 4a) was slightly higher in the high-performance coral phenotype, indicating a higher trophic level, that is, a more carnivorous diet (although only significant between Ed and As, pairwise comparison, $p = 0.013$). This agrees with significantly elevated long-chain monounsaturated fatty acids (df = 3, $F = 1489$, $p < 0.001$, LC MUFA, Figure 4b) and significantly lower contribution of phytoplankton-derived markers compared to animal-derived markers (df = 3, $F = 159.9$, $p < 0.001$, Figure 4c). Phytoplankton markers, by contrast, were higher in the shallow low-performance phenotype (e.g. 20:5(n-3) and 22:6(n-3) with 14%–12% and 4.5%–3.8% in shallow low-performance compared to 7% and 2.5% in deep high-performance phenotypes respectively; Figure 3, Supporting Information Figure S3), indicating a more herbivorous diet. The shallow corals' FATM profiles (Figure 3a) showed a stronger contribution of diatom markers (20:5(n-3), EPA) compared to dinoflagellates markers (22:6(n-3), DHA) across sites (Figures 3a and 4b). However, EPA and DHA were also major compounds of the membranes and other algal markers were less distinct (e.g. 16:1(n-7) or 18:4(n-3) with 4.12 ± 0.84 and 0.87 ± 0.25 in shallow low-performance compared to 6.53 ± 0.61 and 0.57 ± 0.09 in deep high-performance phenotypes respectively). In addition, the contribution of bacterial markers to the individuals' biochemical composition was higher in shallow corals (marginally significant, df = 3, $F = 2.798$, $p = 0.067$), but in general had a negligible overall contribution to the trophic structure.

3.4 | Absolute fatty acid composition, essential fatty acids and potential mobilization and modification of fatty acids

The higher lipid content but lower proportion of PUFA and SFA in deep corals resulted in very similar total PUFA (one-way ANOVA df = 3, $F = 1.621$, $p = 0.216$, 4.38–7.60 mg g AFDW^{-1}) and SFA concentrations (Welch's t-test, df = 3, $F = 2.468$, $p = 0.119$, 3.56–8.24 mg g AFDW^{-1}) across all sites. In contrast, the MUFA content differed significantly with an almost sevenfold change between deep and shallow sites (Kruskal Wallis test, df = 3, $\chi^2 = 12.96$, $p = 0.005$, 3.57 ± 0.95 vs. 24.16 ± 11.43 mg g AFDW^{-1}, Figure 5a–c) dominated by increases in 20:1 and 22:1 fatty acids in deep corals (Figure 3a). Similar clear differences were found in the wax ester content (Kruskal Wallis test, df = 3, $\chi^2 = 12.98$, $p = 0.005$) as well as the storage-to-structural-compound ratio (SFA + MUFA vs. PUFA) that is 2.9-fold enriched in deep corals (one-way ANOVA, $F = 221.6$, $p < 0.001$, Figure 5d,e).

Fatty acid analysis indicated that SFA markers like palmitic acid (PA, 16:0) and stearic acid (SA, 18:0) together with oleic acid (OleA 18:1(n-9)) were enriched in absolute concentration in deep high-performance corals, though not all markers differed significantly between phenotypes (Figure 6, PA: Kruskal Wallis test $p = 0.057$, $\chi^2 = 7.533$, SA: one-way ANOVA $p = 0.090$, $F = 2.488$, OleA: $p = 0.001$, $F = 7.867$). Oleic acid forms one important substrate for n-3 and n-6 PUFA synthesis pathways and their intermediates linoleic acid (LA, 18:2(n-6)) as well as alpha linoleic acid

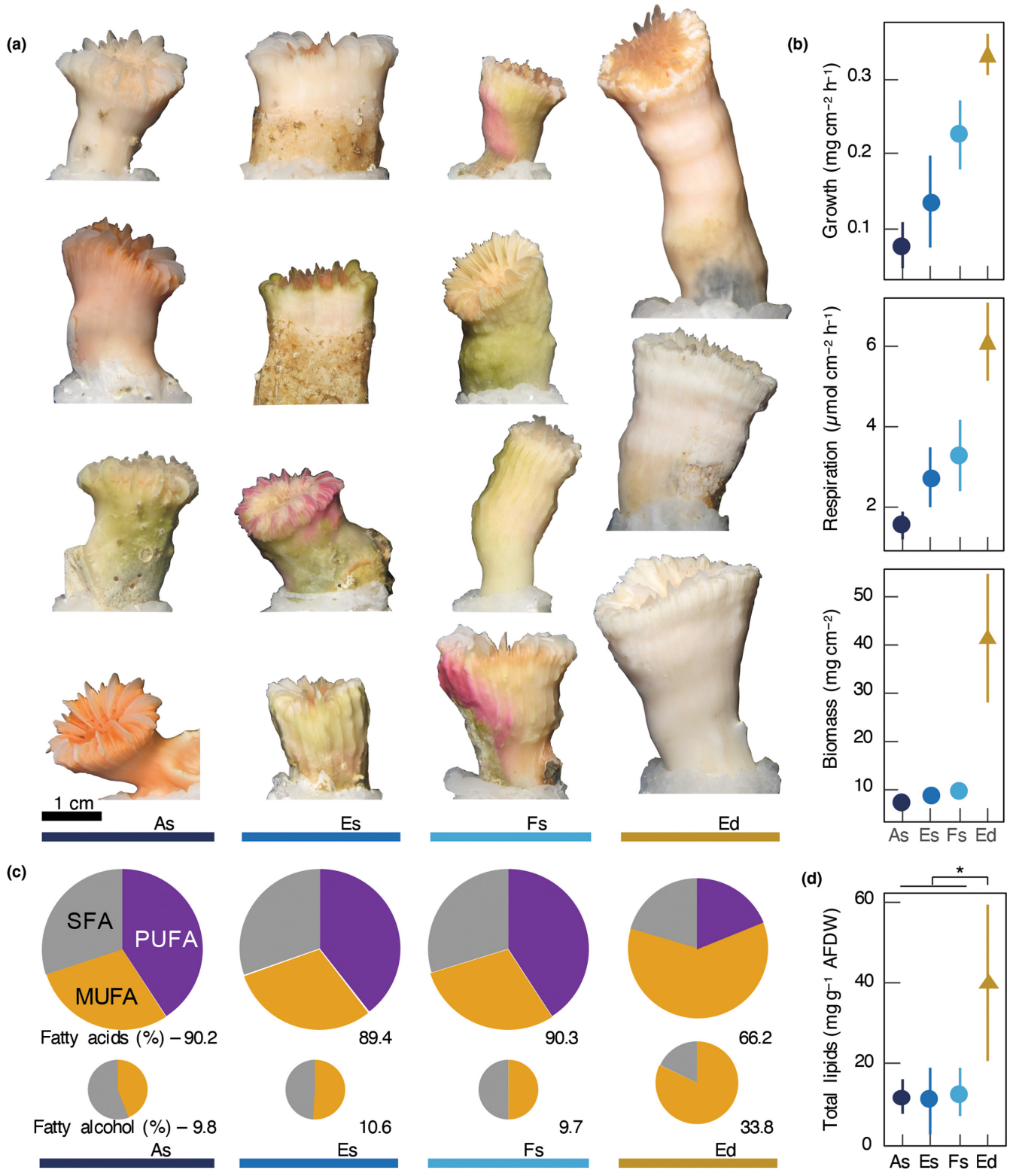

FIGURE 2 Coral phenotype of Desmophyllum dianthus and lipid composition across sites in Comau Fjord, Chile. (a) Coral phenotypes at the shallow sites (first three columns; sites are depicted by dark blue, blue and light blue colour bars) and the deep site (dark yellow horizontal bar). (b) Coral physiological performance traits across sites in terms of growth, respiration and biomass are provided and assessed during September 2016 to August 2017 (Beck et al., 2022). (c) Coral fatty acid trophic marker (FATM) composition is depicted in terms of fatty acids and fatty alcohols (upper and lower panel respectively; circle diameters reflect percentage of fatty acids and fatty alcohols of total lipids at the given sites) and pie charts further indicate their specific composition (SFAs—saturated fatty acid/alcohols (grey), MUFAs—monounsaturated fatty acids/alcohols (orange) and PUFAs—polyunsaturated fatty acids (violet)). (d) The corals' total lipid content across sites. Shallow sites are indicated by As, Es, Fs (coloured in dark blue, blue and light blue respectively) and the deep site by Ed (coloured in dark yellow). Data are mean ± 95% confidence intervals.

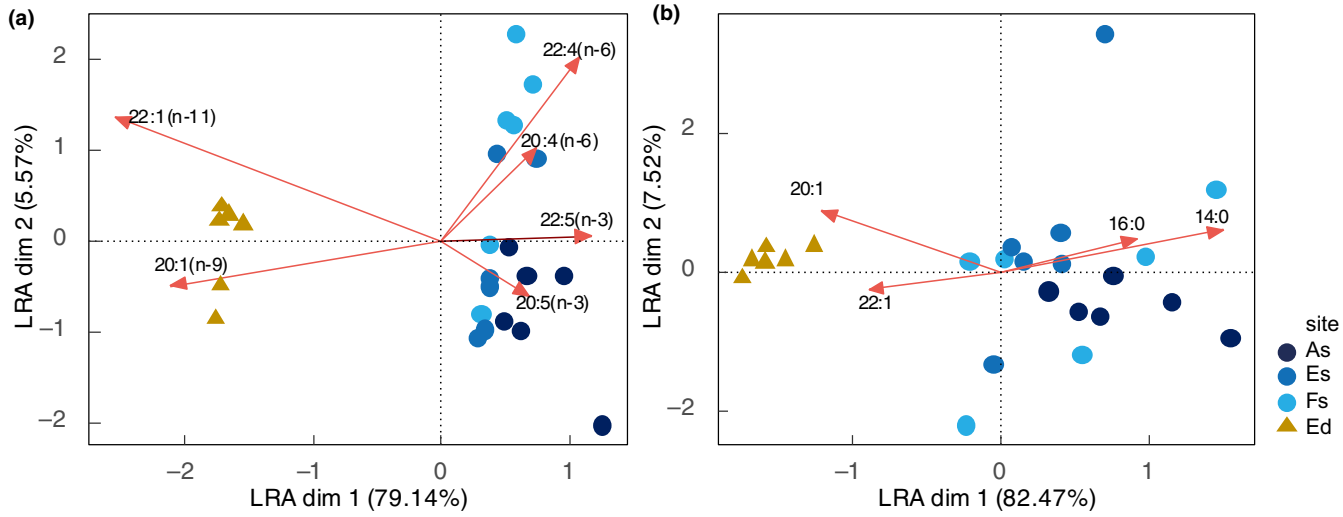

FIGURE 3 Log-ratio analysis (LRA) of the relative fatty acid trophic marker composition of Desmophyllum dianthus. Biplot of LRA of 44 fatty acids (FAs, in (a)) and eight fatty alcohols (Falc, in (b)) in specimens (circles) from four different sites. The LRA dimensions 1 and 2 are differentiated by depth and by within shallow variance respectively. Only markers (FA, Falc) that contribute highly to the separation of the samples are shown in red.

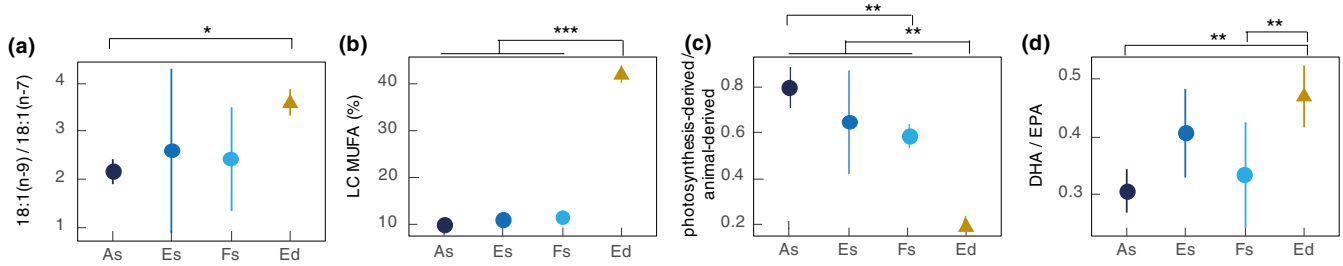

FIGURE 4 Fatty acid trophic marker ratios of Desmophyllum dianthus. Ratio of specific markers across sites provide insights into (a) trophic position 18:1(n-9)/18:1(n-7), (b) herbivore copepod content through sum of long-chain monounsaturated fatty acids (LC MUFA), (c) ratio of phytoplankton versus zooplankton input and trophic network composition (b) DHA/EPA (DHA: docosahexaenoic acid 22:6(n-3), EPA: eicosapentaenoic acid 20:5(n-3)). Data are mean ± 95% confidence intervals. Shallow sites in Comau Fjord (Chile) are indicated by As, Es, Fs and coloured in dark blue, blue and light blue, respectively and the deep site is indicated by Ed and coloured in dark yellow. Significant differences are denoted by *($p \leq 0.05$), **($p \leq 0.01$).

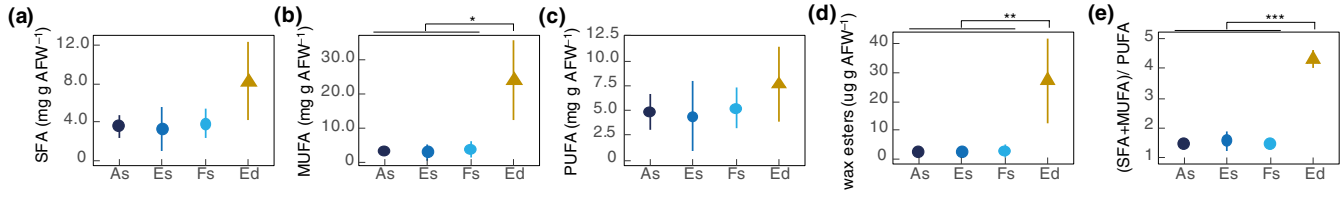

FIGURE 5 Coral fatty acid group concentrations and energy reserves of Desmophyllum dianthus. (a–d) Absolute fatty acid group concentrations (SFA—saturated fatty acid, MUFA—monounsaturated fatty acids and PUFA—polyunsaturated fatty acids) and wax ester content across sites. (e) Fatty acid class ratios reflect the storage capacity ((SFA + MUFA)/PUFA) and are depicted across sites. Shallow sites in Comau Fjord (Chile) are indicated by As, Es, Fs and coloured in dark blue, blue and light blue, respectively and the deep site is indicated by Ed and coloured in dark yellow. Data are mean ± 95% confidence intervals.

(ALA, 18:3(n-3)) were slightly reduced in shallow corals ($p = 0.002$, $F = 6.932$ and $p = 0.066$, $\chi^2 = 7.193$ respectively). While most PUFAs were elevated in deep high-performance phenotypes, some essential PUFAs were remarkably similar across deep and shallow phenotypes (arachidonic acid ARA, 20:4(n-6), $p = 0.29$, $F = 1.338$, adrenic acid AdA 22:4(n-6), $p = 0.115$, $\chi^2 = 5.927$, EPA 20:5(n-3), $p = 0.453$, $F = 0.912$, docosapentaenoic acid DPA 22:5(n-3), $p = 0.879$, $F = 0.224$, Figure 6). Putative health indicators (e.g. EPA/ARA, PUFA(n-3)/PUFA(n-6)) were also very similar in both coral phenotypes (Supporting Information Figure S4).

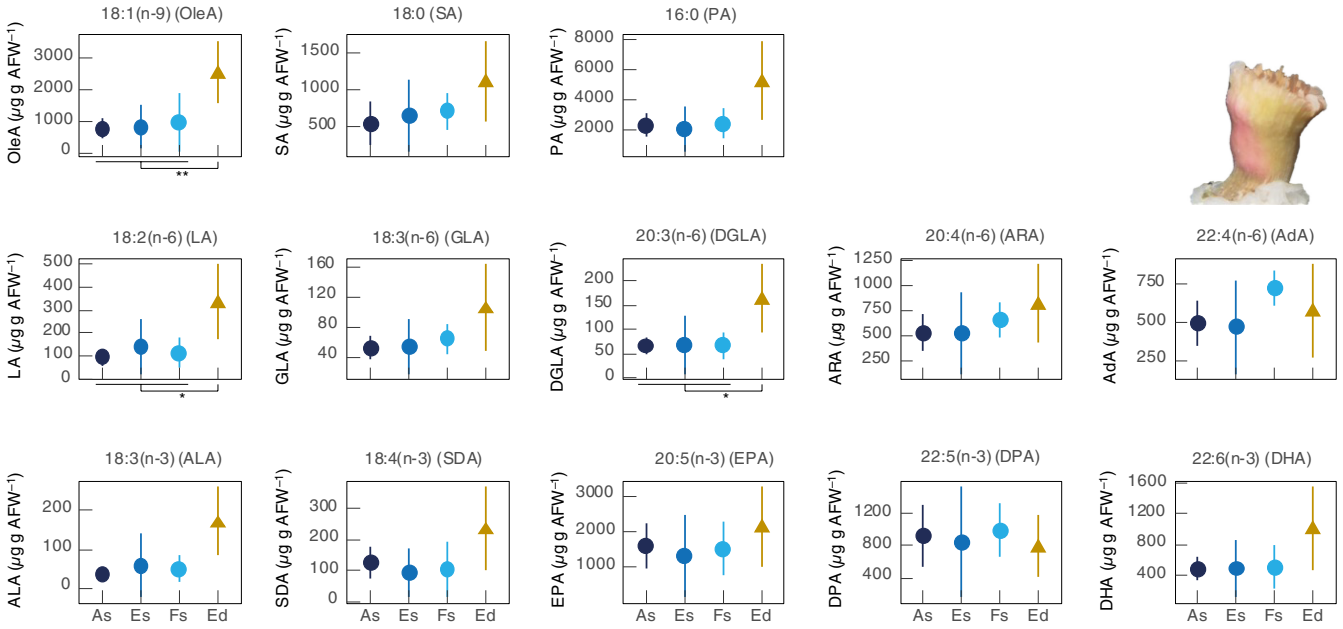

FIGURE 6 Fatty acid concentration through potential biosynthetic pathways of Desmophyllum dianthus. Schematic fatty acid synthesis pathways are provided in the Supplementary Material (Figure S1) and some saturated, monounsaturated and in particular polyunsaturated fatty acids are provided for the different sites (As, Es, Fs and Ed). Shallow sites in Comau Fjord (Chile) are indicated by As, Es, Fs and coloured in dark blue, blue and light blue, respectively and the deep site is indicated by Ed and coloured in dark yellow. For the fatty acids acronyms are used: OleA, oleic acid; SA, stearic acid; PA, palmitic acid; LA, linoleic acid; GLA, gamma-linoleic acid; DGLA, dihomo-gamma-linoleic acid; ARA, arachidonic acid; AdA, adrenic acid; ALA, alpha linoleic acid; SDA, stearidonic acid; EPA, eicosapentaenoic acid; DPA, docosapentaenoic acid; DHA, docosahexaenoic acid. Significant differences are denoted by *($p \leq 0.05$), **($p \leq 0.01$). Data are mean ± 95% confidence intervals.

4 | DISCUSSION

Fatty acid trophic markers in *D. dianthus* clearly distinguish between a deep lipid-rich phenotype and a leaner low-performance phenotype in shallow waters, despite expectedly more challenging conditions like year-round aragonite undersaturation and lower temperature in deep waters (Fillinger & Richter, 2013; Jantzen et al., 2013). Our findings suggest that food is sufficient for the build-up of energy reserves (e.g. wax esters) in deep corals, which is in line with the higher physiological performance and the better health of this coral phenotype (Beck et al., 2022). Potentially, this may be linked to a more carnivorous diet. Shallow water CWCs do not possess the ability to accumulate much energy reserves, underpinning their lower physiological performance (Beck et al., 2022) and potentially subsisting on a more photosynthetically based (phytoplankton) diet. This is in conflict, however, with higher zooplankton abundance and biomass in shallow waters of Comau Fjord (Garcia-Herrera et al., 2022). To resolve this paradox, we link coral performance with FATM data and provide hypotheses explaining the contradictory observations in the context of physico-chemical parameters and resource availability.

4.1 | Trophic network inferences

Overall, the rich biochemical composition of *D. dianthus* supports their omnivore feeding behaviour (Gori et al., 2018; Höfer et al., 2018) similar to other deep-sea corals (Orejas et al., 2001; Rakka et al., 2021). It also clearly indicates differences in prey community between phenotypes from deep and shallow sites, but not along the head-mouth axis of the fjord (Supporting Information Figure S3). As observed for other CWC species (Gori et al., 2018; Naumann et al., 2015; van Oevelen et al., 2018), bacterial markers appear negligible in the fatty acids profile of *D. dianthus*, however, their contribution to the coral's diet is negligible with a slightly larger relative contribution in shallow waters (Supporting Information Figure S3). Phytoplankton and phytodetritus may serve as potential food sources for deep-sea corals (Maier et al., 2019, 2020; Orejas et al., 2001, 2016) and could thus directly account for these specific markers. Phytoplankton inputs are visible through a higher proportion of algal-related markers (EPA, DHA and slightly for 18:4(n-3)), especially in shallow corals (Figure 3a, Supporting Information Figure S3, Dalsgaard et al., 2003; Harwood & Russell, 1984) and the ratio DHA/EPA indicates a diatom prevailed over dinoflagellate signal (Auel et al., 2002; Falk-Petersen et al., 1987; Radice et al., 2019; Scott et al., 2002) across sites (Figure 3a). This also coincides with a predominant pattern of diatom–zooplankton succession rather than dinoflagellate–zooplankton in the plankton communities of Chilean fjords (González et al., 2010; Montero et al., 2017) as reflected in the corals FATM ratio DHA/EPA signal. However, we also need to consider the importance of EPA and DHA as major membrane constituents that will be discussed in more detail below.

Other FATMs, like 14:0, 16:0 (FAs and FAlcs), are also major structural elements in copepods (Boissonnot et al., 2019; Hagen & Auel, 2001) and together with EPA also indicate herbivore copepods. Between depths, however, they differ in relative abundance (Figure 3a,b and Supporting Information Figure S3). The 16:0 fatty alcohol in particular is dominant in shallow corals (Figure 3b) and such short-chained fatty alcohols (similar to FAlc 14:0) are found to be more prevalent in younger copepods and non-calanoids species (e.g. cyclopoid copepods, Kattner et al., 2003; Lischka & Hagen, 2007; Sargent & Falk-Petersen, 1988). The high abundance of small calanoid copepods (e.g. *Paracalanus*, *Clausocalanus*) and cyclopoid copepods in shallow waters of Comau Fjord (Garcia-Herrera et al., 2022) may have accounted for the FATM signal in the shallow corals. Compared to the biomarkers 20:1 and 22:1 (both the FA and FAlc) that are enriched in the tissue of deep corals and their sum used as copepod feeding index (Radice et al., 2019). However, they are mainly synthesized de novo by calanoid copepods (Dalsgaard et al., 2003; Sargent & Whittle, 1981), in particular by the family *Calanidae* (Hagen & Auel, 2001). Despite key calanoid copepods perform diel vertical migration patterns, *Calanidae* are more prevalent in deeper sites while *Metridinidae* occur rather at shallower water layers with limited migration depth (100–200 m, Garcia-Herrera et al., 2022). The low concentration of LC MUFA in shallow corals, may result from these two different dominating families. It has been shown that they have distinct FATM signals in other regions with *Calanus* spp. accumulating 20:1(n-9) and 22:1(n-11) FA and FAlc as major end products compared to *Metridia* spp. with 14:0 and 16:0 FAlc as well as 16:1(n-7) and 18:1(n-9) FA as major end products (Hagen & Auel, 2001). This suggests that even though both groups of zooplankton migrate across several water layers (though at different extent), the family *Calanidae* dominates the deep corals' diet while contributing less to the shallow corals' nutrition.

The trophic marker ratio 18:1(n-9)/18:1(n-7) (Graeve et al., 1997; Legeżyńska et al., 2012) indicates a generally high trophic level in the consumed zooplankton with a higher contribution of carnivorous zooplankton to the diet of the deep high-performance coral phenotype (Figure 4). Thus, algal markers may have resulted from a consumption of herbivorous zooplankton, not by direct phytoplankton uptake and the abundant *Calanidae* signal of deep corals may not necessarily derive from direct consumption. Biomarkers also accumulate at the higher trophic level (Dalsgaard et al., 2003) and it is thus possible that they actually prey on larger zooplankton species that feed on calanoid copepods (Kobari et al., 2021). For instance, mysids as well as *Euchaetidae* are abundant in the deep fjord region and can represent an important food source for deep corals (Garcia-Herrera et al., 2022). *Euchaetidae* are large carnivorous copepods consuming calanoid copepods (Yen, 1985), which could be partly responsible for the calanoid signal. Mysids are in general omnivores (Grossnickle, 1982; Siegfried & Kopache, 1980), while adults may become more carnivorous (Fulton, 1982) and potentially also prey on calanoid copepods (Crescenti, 1997; Díaz-Astudillo et al., 2017).

Overall, the corals' FATM signals can be linked to available zooplankton data and support the dominance of certain zooplankton groups (e.g. *Calanidae* vs. *Metridinidae*, Garcia-Herrera et al., 2022) but we can only speculate whether some markers derive from direct consumption or through accumulation along the food chain. So far, we compared the relative FATM signal without considering absolute values, the clear differences in the corals' energetic status and the differences in coral performance and health status observed across sites. It is also possible that FATM profiles are differently modulated by the organisms in concert with the ecological settings and this may further distort the trophic network signal.

4.2 | Energy availability in the Fjord

Energy availability is an important driver for an organisms' performance and in Comau Fjord, the zooplankton biomass and abundance varies across depths with largest abundances and biomasses in the upper 50 m of the water column (Garcia-Herrera et al., 2022). Thus, shallow water corals should thrive in a land of plenty compared to deep-water corals. Yet this is neither reflected in the directly measured coral traits (Beck et al., 2022, data summarized here in Figure 2), nor in the biochemical signature of the corals. Deep corals have first and foremost approximately fourfold higher lipid content in addition to an elevated ratio of energy storage (SFA + MUFA) to structural (PUFA) FAs as well as 3.4-fold higher wax ester content. Both highlight a thicker coral tissue with high energy storage capacity reflected by the wax ester content in deep corals and provide clear indicators for improved performance. This clearly outlines that measuring the one without the other can result in contrasting conclusions and it is essential to consider the ecological context. There are a number of potential explanations for this food paradox that are not mutually exclusive. It may be possible that (a) shallow organisms grow in denser banks along with a rich community of other suspension and filter feeders, hence experiencing greater competition due to interdependence of competition for space and food (Buss, 1979), (b) exposure to other environmental stressors that have not been evaluated inflict an energetic burden on shallow corals, (c) major differences in plankton biomass and composition exist between the central water column and the plankton close to the steep walls that host the benthic communities (e.g. wall effects) and/or (d) plankton communities represent different food qualities at different locations.

In Chilean fjords, CWCs emerged from the deep and this may be associated with *D. dianthus*' strong phenotypic plasticity and ability to acclimate to very contrasting conditions (Beck et al., 2022; Häussermann et al., 2021). Recent studies suggest that *D. dianthus* in the shallow environments experiences stronger environmental variability and conditions potentially more stressful for corals (Beck et al., 2022). Together with pressures from infestations of their skeleton by microscopic endolithic photo-autotrophs (Försterra et al., 2005; Försterra & Häussermann, 2008; Hassenrück et al., 2013) and other epi- and endolithic organisms (Försterra et al., 2005), the emerged corals may therefore be closer to their physiological limits. Ecological factors may add to this, such as competition. Coral banks in the regions are dominated by *D. dianthus* and

they can be associated with other suspension or filter feeders across depths, for example, brachiopod banks occur from shallow to deep, *Acesta patagonica* co-occurs with *D. dianthus* below 60 m (Fillinger & Richter, 2013; Häussermann et al., 2013), whereas mussel and barnacle banks are restricted to the intertidal (Betti et al., 2017; Häussermann & Försterra, 2009). The shallow waters, however, can be particularly diverse (Försterra et al., 2017) and CWCs co-occur with a myriad of both sessile and mobile species that decrease with depth (Försterra et al., 2005). This probably leads to competition for food and more intense depletion of the plankton community in shallow waters, which may likely be reflected in the low-performance coral phenotype.

Additionally, the strong environmental variability in shallow waters, in particular registered salinity fluctuations (Beck et al., 2022), may affect the plankton composition. For instance, some zooplankton groups are known for their higher salinity tolerance (e.g. Cyclopoida; with known FATM characteristics such as high 16:0 and 14:0 FAlc, 16:0 FA visible in shallow corals, Lischka & Hagen, 2007), whereas others are more sensitive (Magouz et al., 2021). This may also affect the zooplankton abundance (Laprise & Dodson, 1994; Wells et al., 2021), potentially restricting certain zooplankton groups to deeper waters, which lead to more fine-scale distributions and contribute to benthic patchiness. As the available plankton data derive from integrated plankton tows across the upper 50 m of the water column (Garcia-Herrera et al., 2022), they are too coarse to elucidate small-scale patterns and can only serve as first approximations of the shallow zooplankton community.

Zooplankton abundance and biomass diminishes with increasing depth and shallow corals may have a 10-fold higher individual capture rate compared to deeper ones. However, the biomass per prey item increases with depth and may result in a twofold higher prey biomass capture rate (Garcia-Herrera et al., 2022). However, this does not consider prey handling time (small prey vs. few large ones, Sebens, 1982), nor does it include differences in food quality (Dessier et al., 2018; Schaafsma et al., 2018). Certain copepod taxa are rich in energy reserves like wax esters (Dessier et al., 2018; Hagen & Auel, 2001; Schaafsma et al., 2018) causing some copepod genera to have ⅓ lower energy content compared to others (e.g. *Calanus hegolandicus* vs. *Metridia* sp. Or *Temora longicornis*; Dessier et al., 2018). Thus, it may be possible that different calanoid copepod species dominating the deep and shallow corals diet (e.g. *Metridinidae* vs. *Calanidae*, Garcia-Herrera et al., 2022) have potentially very different energy content. While the FATM signal may not be affected, it has consequences for the overall coral fitness and can contribute to the distinct performance observed at different depths.

Sampling bias may also account for some inconsistencies and limit a more precise interpretation of the FATM signal. For instance, plankton tows were performed in the centre of the fjord but the zooplankton community may likely be different closer to the steep fjord walls (Greene et al., 1988; Hirche et al., 2016). Additionally, larger zooplankton and micronekton are mobile and capable of avoiding the nets (Brinton, 1962), but represent import prey items. *Euphausia vallentini* (krill) is common in Comau Fjord (Sánchez et al., 2011) and *D. dianthus* is able to efficiently consume it (Höfer et al., 2018), however, it cannot be properly caught by vertical plankton tows (few young stages & one adult individual; Garcia-Herrera et al., 2022). Similarly, euphausiids employ a number of unique adaptations to entrapped life in fjords and for instance, take advantage of demersal habitats where they exploit a rich and alternative food source compared to their open ocean counterparts (Hamame & Antezana, 2010). Potentially, euphausiids play a critical role in the northern Chilean fjords (Maier et al., 2021), representing an energy-rich diet for deep corals in Comau Fjord (Maier et al., 2021) together with *Euchaetidae* and mysids (Garcia-Herrera et al., 2022). Certain *Euphausiids* can also accumulate wax esters as well as a calanoid signal (like 20:1(n-9) FAlc; Falk-Petersen et al., 2000; Hagen & Auel, 2001). Thus, a revised interpretation of the deep corals' *Calanidae* FATM signal (20:1(n-9) and 22:1(n-11) FA and FAlc) is possible and potentially krill can additionally account for such a signal in deeper sites.

All these mentioned aspects can contribute to the apparent resource limitation and stronger differences in energy availability than originally expected between deep and shallow waters of Comau Fjord. Sampling biases of the available food source, in particular underrepresentation of larger zooplankton groups, can have a direct effect on the interpretation of the FATM signals. Additionally, resource limitation can also result in a modification of fatty acids and a distortion of the FATM signal. In the latter case, the FATM signal may rather be driven by organisms' metabolic needs than their diet. Subsequently, we discuss what we can learn from the physiological background data in terms of energy allocation and finally discuss insights gained from the FATM signal regarding an organisms' potential of active fatty acid modifications.

4.3 | Energy turn-over and performance

Physiological background data support higher net energy available for deep corals, yet they also reveal energetic trade-offs. Energy is channelled into 2.3-fold higher calcification, 5.0-fold higher tissue biomass and 3.4-fold higher energy reserves (e.g. wax esters) in the deep phenotypes, compared to the low-performance shallow phenotype. Energy reserves prevailed through winter in spite of two- to threefold lower zooplankton availability during the cold season (Garcia-Herrera et al., 2022), typical also for other CWC regions (Gaard, 1999; González et al., 2010; Wiborg, 1954). The prevalence is even more remarkable considering the reproduction of *D. dianthus* which, in spite of being energetically costly (Calow, 1979), peaks during austral winter (Feehan et al., 2019). Population genetic analyses indicate a mixed population from shallow to deep sites in Comau Fjord, possibly a source/sink separation and suggest that the deep corals potentially serve as an important source of coral recruits for shallow populations (Addamo et al., 2021). This represents a likely scenario based on our data. Yet it is also plausible that the reduced energy reserves derive from a similar or even higher investment

into reproduction that deplete these reserves in shallow water populations. This may have led to a drop in energy content following the corals' main period of gamete release as has been shown for *Desmophyllum pertusum* (Maier et al., 2020, formerly *Lophelia pertusa*). Physiological trade-offs and shifts in energy allocation are prevalent in an organism's life history and are strategic processes underpinning the success and fitness of organisms, especially under resource limitations (English & Bonsall, 2019; Leuzinger et al., 2012). Under severe limitations there are two possible strategies: (a) invest in reproduction at the risk of death or (b) invest into somatic growth to endure periods of scarcity (Fischer et al., 2009; Stearns, 1989). In a tropical coral (*Montipora digitata*), resource limitations led to a substantial reduction in somatic growth while calcification and reproduction was maintained and energy transfer increased. However, under severe resource scarcity, reproduction was halted but growth maintained to some extent in the same study (Leuzinger et al., 2012). Applied to our study, this could mean that somatic growth (in terms of reduced biomass: Figure 2b, or in some corals with lower tissue cover: Beck et al., 2022) is sacrificed to maintain calcification and reproduction. While we do see such higher energy transfer into growth, investment into reproduction requires further investigation. However, such physiological trade-offs likely require the mobilization of energy reserves and may contribute to the distortion of the FATM profiles, which must be taken into account.

4.4 | Fatty acid indicators of organism health status and functionality

Despite clear differences in total lipids as well as energy storage capacity (Figures 2 and 5e), the similar total PUFA concentration among sites and depths is striking (Figure 5c). It may represent the corals' dependencies on specific concentrations of essential fatty acids for their general metabolic regulation and suggests the need to maintain them across sites regardless of the environmental conditions. Polyunsaturated FA are key molecules for metabolic regulation and support structural integrity, membrane functioning and immune system competency (Kim et al., 2021; Russo, 2009; Tocher, 2003). Invertebrates have been found to metabolize SFA and MUFA under stressful conditions, while preserving PUFA as long as possible (Mezek et al., 2010; Schlechtriem et al., 2008). Here we also find very low MUFA content in shallow corals but similar PUFA content, in line with the lower performance in shallow water and likely limiting conditions in shallow water. Thus, the low-performance corals need to mobilize fatty acids like MUFAs to fuel their metabolism. Marked differences in absolute lipid concentration can, thus, result in an over-representation of these essential lipids in the relative FATM profiles (e.g. algal markers like EPA, ARA in shallow corals, Figure 3c). In turn, it may potentially also result in a lack of certain markers (e.g. LC MUFAs like Calanidae markers 20:1(n-9)) that were readily metabolized to fuel the organisms' metabolic demands. This clearly shows the duality of some FA markers, that is, the dietary origin and the modification through their catabolism (fatty acid integration 'black box', Galloway & Budge, 2020; Helenius et al., 2020; Kabeya et al., 2020).

Underlying drivers for such modified levels may be selective retention of essential FAs (Yasuda et al., 2021), trophic upgrading (Helenius et al., 2020) or de novo synthesis by the coral (Kabeya et al., 2018). The significantly lower linoleic acid (LA, 18:2(n-6)) and reduced ALA (18:3(n-3)) concentration may indicate their trophic upgrading into LC PUFAs (Figure 5), but it may also be possible that *D. dianthus* is capable of de novo synthesis following all PUFA biosynthesis steps (Figure 6) through the activity of methyl-end desaturation (Δ12, Δ15) enzymes (Kabeya et al., 2018). For example, *Desmophyllum pertusum* a sibling species is able to synthesize essential fatty acids de novo including PUFA(n-3) (EPA and DHA) (Mueller et al., 2014). Similar observations exist for tropical corals, where the two essential PUFAs (LA and ALA) were identified (Kabeya et al., 2018). Yet, the energetic costs and the potential rate of modification (that may still be limited in animals) of this de novo synthesis need to be evaluated. Besides, a capability does not necessarily indicate its activity and chronic stress, for example, eutrophication, has been shown to actually limit the ability for lipid synthesis in tropical corals (Kim et al., 2021).

Notably, fatty acid modifications can be linked to organism performance and in tropical corals, PUFA ratios (e.g. DHA:EPA, EPA:ARA) were employed as indicators for water quality as well as putative coral health status (Kim et al., 2021; Rocker et al., 2019). In this study, these putative health indicators did not differ markedly (e.g. n-3:n-6 PUFA, EPA:ARA) despite clear performance differences, which potentially suggests strong modification in low-performance corals to reach similar levels as in high-performance corals. Thus, we would expect that the FATM profile of the fit deep coral phenotype more closely resembles their diet, while the limiting conditions in shallow waters warrant further investigation of the corals' fatty acid metabolism and thus potentially stronger modification of their FATM profile, especially following winter. This also adds caution to the interpretation of the FATM profiles from other CWC species, in particular from areas with distinct and low background productivity (first insights and comparisons are provided in the Supporting Information Appendix S1). Analogous to studies in tropical corals (Kim et al., 2021; Rocker et al., 2019)-specific PUFA ratios may rather be used as putative health indicators in CWCs with the ability to differentiate optimal versus suboptimal environmental conditions, but this will require more detailed experimental studies to support such application in *D. dianthus* as well as other benthic suspension feeders.

5 | CONCLUSIONS

In the past, FA profiles in CWCs and other benthic suspension feeders helped to gain insight into their trophic ecology and the ecological setting they flourish in. This led to the identification of contrasting productivity areas. Yet, no previous study has combined in situ sampling with physiological investigations to understand how physiological limitations due to differences in food availability modulate the biochemistry in CWCs. Here, FATMs provide insights

into the corals' potential in situ food sources, but we also emphasize the need for a more holistic view and better integration of physiological (metabolic rates, performance, fitness) and ecological information (e.g. food availability and sources, potential stressors) with FATM analysis. While FATM and lipid content analyses gained a whole new perspective on coral performance in Comau Fjord, it also revealed numerous open questions that warrant further investigations. In this respect, the Comau Fjord represents an ideal natural laboratory that allows the design of experiments able to trace lipid metabolism and energy allocation pathways in benthic suspension feeders that can help to identify more refined health markers. Such biomarkers are key to assess the health status of organisms inhabiting more remote and deep-sea environments. This will further provide a more precise understanding of benthic foundation species, like CWCs, and their ability to cope with future changing conditions in particular under contrasting and changing productivity regimes.

AUTHOR CONTRIBUTIONS

Gertraud M. Schmidt-Grieb, Jürgen Laudien and Claudio Richter designed the study. Jürgen Laudien, Günter Försterra and Gertraud M. Schmidt-Grieb contributed background information and collected the corals. Marlene Wall, Matthias Woll and Kristina K. Beck conducted the coral preparation and lipid measurements. Kristina K. Beck and Gertraud M. Schmidt-Grieb contributed physiological background data. Marlene Wall and Matthias Woll analysed raw data. Marlene Wall and Martin Graeve interpreted the data. Marlene Wall conducted the statistical analysis. Together with Kristina K. Beck and Marlene Wall prepared the figures. Marlene Wall and Claudio Richter wrote the first draft of the paper. All authors contributed to the final discussion and edited the manuscript.

ACKNOWLEDGEMENTS

Corals were collected in the field within the coral sample permit assigned to the Fundación San Ignacio de Huinay. Export permits for *Desmophyllum dianthus* according to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) were admitted by the Chilean Servicio Nacional de Pesca y Acuicultura (Sernapesca; Permiso CITES N° 17000003WS) and import permits by the German Federal Agency for Nature Conservation (BfN) (E 00134/17). We thank Esther Lüdtke for laboratory assistance and Alexandra Kler Lago for the analysis of the coral pictures. We express our deepest thanks to the scientific SCUBA divers (Aurelia Reichardt, Lea Happel and Maximilian Neffe) and Henning Schröder for assistance during the field work for this study. We are also very grateful for the help we received from the staff of the Fundación San Ignacio del Huinay (particularly Ulrich Pörschmann, Stacy Ballyram, Francine Beaujot and Insa Stolz) during field work in Comau Fjord. Open Access funding enabled and organized by Projekt DEAL.

FUNDING INFORMATION

This study was initiated within the bilateral Chilean-German project PACOC (Plankton- and cold-water coral ecology in the Comau Fjord, Chile; CONICYT-BMBF: 20140041, 01DN15024), CONICYT FONDAP-IDEAL 15150003 as well as PACES II-T1WP6 and Changing Earth—Sustaining our Future: Subtopics 4.2 and 6.1 at AWI. Finally, additional funding was provided through the AWI strategy fund DACCOR (Deciphering the Antarctic cold-water coral record; #IP74010002).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data are available from Pangaea Data Repository: https://doi.org/10.1594/PANGAEA.962593 & https://doi.org/10.1594/PANGAEA.962841 (Wall et al., 2023a, 2023b).

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REFERENCES

Addamo, A. M., Zaccara, S., Försterra, G., Höfer, J., García-Jiménez, R., Crosa, G., & Machordom, A. (2021). Genetic conservation management of marine resources and ecosystems of Patagonian fjords. *Frontiers in Marine Science*, *8*, 612195. https://doi.org/10.3389/fmars.2021.612195

Auel, H., Harjes, M., da Rocha, R., Stübing, D., & Hagen, W. (2002). Lipid biomarkers indicate different ecological niches and trophic relationships of the Arctic hyperiid amphipods *Themisto abyssorum* and *T. libellula*. *Polar Biology*, *25*(5), 374–383. https://doi.org/10.1007/s00300-001-0354-7

Beck, K., Schmidt-Grieb, G., Laudien, J., Försterra, G., Häussermannn, V., González, H., Espinoza, J., Richter, C., & Wall, M. (2022). Environmental stability and phenotypic plasticity benefit the cold-water coral *Desmophyllum dianthus* in an acidified fjord. *Communications Biology*, *5*(1), 683. in press.

Betti, F., Bavestrello, G., Bo, M., Enrichetti, F., Loi, A., Wanderlingh, A., Pérez-Santos, I., & Daneri, G. (2017). Benthic biodiversity and ecological gradients in the Seno Magdalena (Puyuhuapi Fjord, Chile). *Estuarine, Coastal and Shelf Science*, *198*, 269–278. https://doi.org/10.1016/j.ecss.2017.09.018

Boissonnot, L., Niehoff, B., Ehrenfels, B., Søreide, J., Hagen, W., & Graeve, M. (2019). Lipid and fatty acid turnover of the pteropods *Limacina helicina*, *L. retroversa* and *Clione limacina* from Svalbard waters. *Marine Ecology Progress Series*, *609*, 133–149. https://doi.org/10.3354/meps12837

Boschker, H. T. S., & Middelburg, J. J. (2002). Stable isotopes and biomarkers in microbial ecology. *FEMS Microbiology Ecology*, *40*(2), 85–95. https://doi.org/10.1111/j.1574-6941.2002.tb00940.x

Brett, M. T., Müller-Navarra, D. C., Ballantyne, A. P., Ravet, J. L., & Goldman, C. R. (2006). *Daphnia* fatty acid composition reflects that of their diet. *Limnology and Oceanography*, *51*(5), 2428–2437. https://doi.org/10.4319/lo.2006.51.5.2428

Brinton, E. (1962). *Variable factors affecting the apparent range and estimated concentration of Euphausiids in the North Pacific* (pp. 375–408). *Pacific Science*.

Budge, S. M., Iverson, S. J., & Koopman, H. N. (2006). Studying trophic ecology in marine ecosystems using fatty acids: A primer on analysis and interpretation. *Marine Mammal Science*, *22*(4), 759–801. https://doi.org/10.1111/j.1748-7692.2006.00079.x

Buhl-Mortensen, L., & Mortensen, P. B. (2004). Symbiosis in deep-water corals. *Symbioses*, *37*, 33–61.

Bureau, D., Kaushik, S., & Cho, C. Y. (2002). *Bioenergetics*.

Büscher, J. V., Form, A. U., & Riebesell, U. (2017). Interactive effects of ocean acidification and warming on growth, fitness and survival of the cold-water coral *Lophelia pertusa* under different food availabilities. *Frontiers in Marine Science*, *4*, 101. https://doi.org/10.3389/fmars.2017.00101

Büscher, J. V., Wisshak, M., Form, A. U., Titschack, J., Nachtigall, K., & Riebesell, U. (2019). *In situ* growth and bioerosion rates of *Lophelia pertusa* in a Norwegian fjord and open shelf cold-water coral habitat. *PeerJ*, *7*, e7586. https://doi.org/10.7717/peerj.7586

Buss, L. W. (1979). Bryozoan overgrowth interactions—The interdependence of competition for space and food. *Nature*, *281*(5731), Article 5731. https://doi.org/10.1038/281475a0

Calow, P. (1979). The cost of reproduction—A physiological approach. *Biological Reviews*, *54*(1), 23–40. https://doi.org/10.1111/j.1469-185X.1979.tb00866.x

Carlier, A., Le Guilloux, E., Olu, K., Sarrazin, J., Mastrototaro, F., Taviani, M., & Clavier, J. (2009). Trophic relationships in a deep Mediterranean cold-water coral bank (Santa Maria di Leuca, Ionian Sea). *Marine Ecology Progress Series*, *397*, 125–137. https://doi.org/10.3354/meps08361

Crescenti, N. (1997). Mysids. In L. Guglielmo & A. Ianora (Eds.), *Atlas of marine zooplankton straits of magellan: Amphipods, Euphausiids, Mysids, ostracods, and Chaetognaths* (pp. 131–156). Springer. https://doi.org/10.1007/978-3-642-60340-2_5

Dalsgaard, J., St. John, M., Kattner, G., Müller-Navarra, D., & Hagen, W. (2003). Fatty acid trophic markers in the pelagic marine environment. In *Advances in marine biology* (Vol. *46*, pp. 225–340). Elsevier. https://doi.org/10.1016/S0065-2881(03)46005-7

Dessier, A., Dupuy, C., Kerric, A., Mornet, F., Authier, M., Bustamante, P., & Spitz, J. (2018). Variability of energy density among mesozooplankton community: New insights in functional diversity to forage fish. *Progress in Oceanography*, *166*, 121–128. https://doi.org/10.1016/j.pocean.2017.10.009

Díaz-Astudillo, M., Cáceres, M. A., & Landaeta, M. F. (2017). Zooplankton structure and vertical migration: Using acoustics and biomass to compare stratified and mixed fjord systems. *Continental Shelf Research*, *148*, 208–218. https://doi.org/10.1016/j.csr.2017.09.004

Dodds, L., Black, K., Orr, H., & Roberts, J. (2009). Lipid biomarkers reveal geographical differences in food supply to the cold-water coral *Lophelia pertusa* (Scleractinia). *Marine Ecology Progress Series*, *397*, 113–124. https://doi.org/10.3354/meps08143

Dorey, N., Gjelsvik, Ø., Kutti, T., & Büscher, J. V. (2020). Broad thermal tolerance in the cold-water coral *Lophelia pertusa* from Arctic and boreal reefs. *Frontiers in Physiology*, *10*, 1636. https://doi.org/10.3389/fphys.2019.01636

Duineveld, G., Jeffreys, R., Lavaleye, M., Davies, A., Bergman, M., Watmough, T., & Witbaard, R. (2012). Spatial and tidal variation in food supply to shallow cold-water coral reefs of the Mingulay Reef complex (Outer Hebrides, Scotland). *Marine Ecology Progress Series*, *444*, 97–115. https://doi.org/10.3354/meps09430

Duineveld, G., Lavaleye, M., & Berghuis, E. (2004). Particle flux and food supply to a seamount cold-water coral community (Galicia Bank, NW Spain). *Marine Ecology Progress Series*, *277*, 13–23. https://doi.org/10.3354/meps277013

English, S., & Bonsall, M. B. (2019). Physiological dynamics, reproduction-maintenance allocations, and life history evolution. *Ecology and Evolution*, *9*(16), 9312–9323. https://doi.org/10.1002/ece3.5477

Falk-Petersen, S., Hagen, W., Kattner, G., Clarke, A., & Sargent, J. (2000). Lipids, trophic relationships, and biodiversity in Arctic and Antarctic krill. *Canadian Journal of Fish and Aquaculture Science*, *57*, 178–191.

Falk-Petersen, S., Sargent, J. R., & Tande, K. S. (1987). Lipid composition of zooplankton in relation to the sub-arctic food web. *Polar Biology*, *8*(2), 115–120. https://doi.org/10.1007/BF00297065

Feehan, K. A., Waller, R. G., & Häussermann, V. (2019). Highly seasonal reproduction in deep-water emergent *Desmophyllum dianthus* (Scleractinia: Caryophylliidae) from the Northern Patagonian fjords. *Marine Biology*, *166*(4), 52. https://doi.org/10.1007/s00227-019-3495-3

Fillinger, L., & Richter, C. (2013). Vertical and horizontal distribution of *Desmophyllum dianthus* in Comau Fjord, Chile: A cold-water coral thriving at low pH. *PeerJ*, *1*, e194. https://doi.org/10.7717/peerj.194

Fischer, B., Taborsky, B., & Dieckmann, U. (2009). Unexpected patterns of plastic energy allocation in stochastic environments. *The American Naturalist*, *173*(3), E108–E120. https://doi.org/10.1086/596536

Folch, J., Lees, M., & Stanley, G. H. S. (1957). A simple method for the isolation and purification of total lipides from animal tissues. *Journal of Biological Chemistry*, *226*(1), 497–509. https://doi.org/10.1016/S0021-9258(18)64849-5

Foley, N. S., van Rensburg, T. M., & Armstrong, C. W. (2010). The ecological and economic value of cold-water coral ecosystems. *Ocean & Coastal Management*, *53*(7), 313–326. https://doi.org/10.1016/j.ocecoaman.2010.04.009

Försterra, G., Beuck, L., Häussermann, V., & Freiwald, A. (2005). Shallow-water Desmophyllum dianthus (Scleractinia) from Chile: Characteristics of the biocoenoses, the bioeroding community, heterotrophic interactions and (paleo)-bathymetric implications. In A. Freiwald & J. M. Roberts (Eds.), *Cold-water corals and ecosystems* (pp. 937–977). Springer-Verlag. https://doi.org/10.1007/3-540-27673-4_48

Försterra, G., & Häussermann, V. (2008). Unusual symbiotic relationships between microendolithic phototrophic organisms and azooxanthellate cold-water corals from Chilean fjords. *Marine Ecology Progress Series*, *370*, 121–125. https://doi.org/10.3354/meps07630

Försterra, G., Häussermann, V., & Laudien, J. (2017). Animal forests in the Chilean fjords: Discoveries, perspectives, and threats in shallow and deep waters. In S. Rossi, L. Bramanti, A. Gori, & C. Orejas (Eds.), *Marine animal forests* (pp. 277–313). Springer International Publishing. https://doi.org/10.1007/978-3-319-21012-4_3

Fosså, J. H., Mortensen, P. B., & Furevik, D. M. (2002). The deep-water coral *Lophelia pertusa* in Norwegian waters: Distribution and fishery impacts. *Hydrobiologia*, *471*, 1–12.

Fulton, R. S. (1982). Predatory feeding of two marine mysids. *Marine Biology*, *72*(2), 183–191. https://doi.org/10.1007/BF00396919

Gaard, E. (1999). The zooplankton community structure in relation to its biological and physical environment on the Faroe shelf, 1989–1997. *Journal of Plankton Research*, *21*(6), 1133–1152. https://doi.org/10.1093/plankt/21.6.1133

Galloway, A. W. E., & Budge, S. M. (2020). The critical importance of experimentation in biomarker-based trophic ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1804), 20190638. https://doi.org/10.1098/rstb.2019.0638

Garcia-Herrera, N., Cornils, A., Laudien, J., Niehoff, B., Höfer, J., Försterra, G., González, H. E., & Richter, C. (2022). Seasonal and diel variations in the vertical distribution, composition, abundance and biomass of zooplankton in a deep Chilean Patagonian fjord. *PeerJ*, *10*, e12823.

Georgian, S. E., Dupont, S., Kurman, M., Butler, A., Strömberg, S. M., Larsson, A. I., & Cordes, E. E. (2016). Biogeographic variability in the physiological response of the cold-water coral *Lophelia pertusa* to ocean acidification. *Marine Ecology*, *37*(6), 1345–1359. https://doi.org/10.1111/maec.12373

Gili, J.-M., & Coma, R. (1998). Benthic suspension feeders: their paramount role in littoral marine food webs. *Trends in Ecology & Evolution*, *13*(8), 316–321.

González, H., Calderón, M., Castro, L., Clement, A., Cuevas, L., Daneri, G., Iriarte, J., Lizárraga, L., Martínez, R., Menschel, E., Silva, N., Carrasco, C., Valenzuela, C., Vargas, C., & Molinet, C. (2010). Primary production and plankton dynamics in the Reloncaví Fjord and the Interior Sea of Chiloé, Northern Patagonia, Chile. *Marine Ecology Progress Series*, *402*, 13–30. https://doi.org/10.3354/meps08360

Gori, A., Ferrier-Pagès, C., Hennige, S. J., Murray, F., Rottier, C., Wicks, L. C., & Roberts, J. M. (2016). Physiological response of the cold-water coral *Desmophyllum dianthus* to thermal stress and ocean acidification. *PeerJ*, *4*, e1606. https://doi.org/10.7717/peerj.1606

Gori, A., Tolosa, I., Orejas, C., Rueda, L., Viladrich, N., Grinyó, J., Flögel, S., Grover, R., & Ferrier-Pagès, C. (2018). Biochemical composition of the cold-water coral *Dendrophyllia cornigera* under contrasting productivity regimes: Insights from lipid biomarkers and compound-specific isotopes. *Deep Sea Research Part I: Oceanographic Research Papers*, *141*, 106–117. https://doi.org/10.1016/j.dsr.2018.08.010

Graeve, M., & Greenacre, M. J. (2020). The selection and analysis of fatty acid ratios: A new approach for the univariate and multivariate analysis of fatty acid trophic markers in marine pelagic organisms. *Limnology and Oceanography: Methods*, *18*(5), 196–210. https://doi.org/10.1002/lom3.10360

Graeve, M., Kattner, G., & Piepenburg, D. (1997). Lipids in Arctic benthos: Does the fatty acid and alcohol composition reflect feeding and trophic interactions? *Polar Biology*, *18*(1), 53–61. https://doi.org/10.1007/s003000050158

Greenacre, M. J. (2018). *Compositional data analysis in practice*. CRC Press.

Greene, C. H., Wiebe, P. H., Burczynski, J., & Youngbluth, M. J. (1988). Acoustical detection of high-density krill demersal layers in the submarine canyons off Georges Bank. *Science*, *241*(4863), 359–361. https://doi.org/10.1126/science.241.4863.359

Grossnickle, N. E. (1982). Feeding habits ofMysis relicta—An overview. In M. D. Morgan (Ed.), *Ecology of Mysidacea* (pp. 101–107). Springer. https://doi.org/10.1007/978-94-009-8012-9_11

Gu, Z., Eils, R., & Schlesner, M. (2016). Complex heatmaps reveal patterns and correlations in multidimensional genomic data. *Bioinformatics.*, *32*, 2847–2849.

Hagen, W., & Auel, H. (2001). Seasonal adaptations and the role of lipids in oceanic zooplankton. *Zoology*, *104*(3–4), 313–326. https://doi.org/10.1078/0944-2006-00037

Hamame, M., & Antezana, T. (2010). Vertical diel migration and feeding of *Euphausia vallentini* within southern Chilean fjords. *Deep Sea Research Part II: Topical Studies in Oceanography*, *57*(7–8), 642–651. https://doi.org/10.1016/j.dsr2.2009.10.013

Harwood, J. L., & Russell, N. J. (1984). Major lipid types in plants and micro-organisms. In *Lipids in plants and microbes* (pp. 7–34). Springer. https://doi.org/10.1007/978-94-011-5989-0_2

Hassenrück, C., Jantzen, C., Försterra, G., Häussermann, V., & Willenz, P. (2013). Rates of apical septal extension of *Desmophyllum dianthus*: Effect of association with endolithic photo-autotrophs. *Marine Biology*, *160*(11), 2919–2927. https://doi.org/10.1007/s00227-013-2281-x

Häussermann, V., Ballyram, S. A., Försterra, G., Cornejo, C., Ibáñez, C. M., Sellanes, J., Thomasberger, A., Espinoza, J. P., & Beaujot, F. (2021). Species that fly at a higher game: patterns of deep–water emergence along the Chilean coast, including a global review of the phenomenon. *Frontiers in Marine Science*, *8*, 688316. https://doi.org/10.3389/fmars.2021.688316

Häussermann, V., & Försterra, G. (2009). *Marine benthic fauna of Chilean Patagonia*. Nature. in Focus. Patagonia Marina.

Häussermann, V., Försterra, G., Melzer, R. R., & Meyer, R. (2013). Gradual changes of benthic biodiversity in Comau Fjord, Chilean Patagonia—Lateral observations over a decade of taxonomic research. *Spixiana*, *36*, 161–171.

Helenius, L., Budge, S. M., Nadeau, H., & Johnson, C. L. (2020). Ambient temperature and algal prey type affect essential fatty acid incorporation and trophic upgrading in a herbivorous marine copepod. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1804), 20200039. https://doi.org/10.1098/rstb.2020.0039

Hennige, S. J., Wicks, L. C., Kamenos, N. A., Perna, G., Findlay, H. S., & Roberts, J. M. (2015). Hidden impacts of ocean acidification to live and dead coral framework. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1813), 20150990. https://doi.org/10.1098/rspb.2015.0990

Hirche, H.-J., Laudien, J., & Buchholz, F. (2016). Near-bottom zooplankton aggregations in Kongsfjorden: Implications for pelago–benthic coupling. *Polar Biology*, *39*(10), 1897–1912. https://doi.org/10.1007/s00300-015-1799-4

Höfer, J., González, H. E., Laudien, J., Schmidt, G. M., Häussermann, V., & Richter, C. (2018). All you can eat: The functional response of the cold-water coral *Desmophyllum dianthus* feeding on krill and copepods. *PeerJ*, *6*, e5872. https://doi.org/10.7717/peerj.5872

Imbs, A. B., Dang, L. P. T., & Nguyen, K. B. (2019). Comparative lipidomic analysis of phospholipids of hydrocorals and corals from tropical and cold-water regions. *PLOS One*, *14*(4), e0215759. https://doi.org/10.1371/journal.pone.0215759

Imbs, A. B., & Yakovleva, I. M. (2012). Dynamics of lipid and fatty acid composition of shallow-water corals under thermal stress: An experimental approach. *Coral Reefs*, *31*(1), 41–53. https://doi.org/10.1007/s00338-011-0817-4

Ingels, J., Vanreusel, A., Brandt, A., Catarino, A. I., David, B., Ridder, C. D., Dubois, P., Gooday, A. J., Martin, P., Pasotti, F., & Robert, H. (2012). Possible effects of global environmental changes on Antarctic benthos: a synthesis across five major taxa. *Ecology and Evolution*, *2*, 453–485.

Jantzen, C., Laudien, J., Sokol, S., Försterra, G., Häussermann, V., Kupprat, F., & Richter, C. (2013). In situ short-term growth rates of a cold-water coral. *Marine and Freshwater Research*, *64*(7), 631. https://doi.org/10.1071/MF12200

Jokiel, P., Maragos, J. E., & Franzisket, L. (1978). Coral growth: Buoyant weight technique. In D. R. Stoddart & R. E. Johannes (Eds.), *Coral reefs: Research methods*, 5. UNESCO.

Joseph, J. D. (1979). Lipid composition of marine and estuarine invertebrates: Porifera and cnidaria. *Progress in Lipid Research*, *18*(1), 1–30. https://doi.org/10.1016/0163-7827(79)90002-X

Kabeya, N., Fonseca, M. M., Ferrier, D. E. K., Navarro, J. C., Bay, L. K., Francis, D. S., Tocher, D. R., Castro, L. F. C., & Monroig, Ó. (2018). Genes for de novo biosynthesis of omega-3 polyunsaturated fatty acids are widespread in animals. *Science Advances*, *4*(5), eaar6849. https://doi.org/10.1126/sciadv.aar6849

Kabeya, N., Gür, İ., Oboh, A., Evjemo, J. O., Malzahn, A. M., Hontoria, F., Navarro, J. C., & Monroig, Ó. (2020). Unique fatty acid desaturase capacities uncovered in *Hediste diversicolor* illustrate the roles of aquatic invertebrates in trophic upgrading. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1804), 20190654. https://doi.org/10.1098/rstb.2019.0654

Kattner, G., Albers, C., Graeve, M., & Schnack-Schiel, S. B. (2003). Fatty acid and alcohol composition of the small polar copepods, *Oithona* and *Oncaea*: Indication on feeding modes. *Polar Biology*, *26*(10), 666–671. https://doi.org/10.1007/s00300-003-0540-x

Kattner, G., & Fricke, H. S. G. (1986). Simple gas–liquid chromatographic method for the simultaneous determination of fatty acids and alcohols in wax esters of marine organisms. *Journal of Chromatography A*, *361*, 263–268. https://doi.org/10.1016/S0021-9673(01)86914-4

Kim, T., Lee, J. C. Y., Kang, D.-H., Duprey, N. N., Leung, K. S., Archana, A., & Baker, D. M. (2021). Modification of fatty acid profile and biosynthetic pathway in symbiotic corals under eutrophication. *Science of*

the Total Environment, *771*, 145336. https://doi.org/10.1016/j.scitotenv.2021.145336

Kiriakoulakis, K., Fisher, E., Wolff, G. A., Freiwald, A., Grehan, A., & Roberts, J. M. (2005). Lipids and nitrogen isotopes of two deep-water corals from the North-East Atlantic: Initial results and implications for their nutrition. In A. Freiwald & J. M. Roberts (Eds.), *Cold-water corals and ecosystems* (pp. 715–729). Springer. https://doi.org/10.1007/3-540-27673-4_37

Kobari, T., Tokumo, Y., Sato, I., Kume, G., & Hirai, J. (2021). Metabarcoding analysis of trophic sources and linkages in the plankton community of the Kuroshio and neighboring waters. *Scientific Reports*, *11*(1), 23265. https://doi.org/10.1038/s41598-021-02083-8

Laprise, R., & Dodson, J. J. (1994). Environmental variability as a factor controlling spatial patterns in distribution and species diversity of zooplankton in the St. Lawrence Estuary. *Marine Ecology Progress Series*, *107*(67–81), 15.

Larsson, A., Lundälv, T., & van Oevelen, D. (2013). Skeletal growth, respiration rate and fatty acid composition in the cold-water coral *Lophelia pertusa* under varying food conditions. *Marine Ecology Progress Series*, *483*, 169–184. https://doi.org/10.3354/meps10284

Legeżyńska, J., Kędra, M., & Walkusz, W. (2012). When season does not matter: Summer and winter trophic ecology of Arctic amphipods. *Hydrobiologia*, *684*(1), 189–214. https://doi.org/10.1007/s10750-011-0982-z

Leuzinger, S., Willis, B. L., & Anthony, K. R. N. (2012). Energy allocation in a reef coral under varying resource availability. *Marine Biology*, *159*(1), 177–186. https://doi.org/10.1007/s00227-011-1797-1

Lischka, S., & Hagen, W. (2007). Seasonal lipid dynamics of the copepods Pseudocalanus minutus (Calanoida) and Oithona similis (Cyclopoida) in the Arctic Kongsfjorden (Svalbard). *Marine Biology*, *150*(3), 443–454. https://doi.org/10.1007/s00227-006-0359-4

Magouz, F. I., Essa, M. A., Matter, M., Mansour, A. T., Gaber, A., & Ashour, M. (2021). Effect of different salinity levels on population dynamics and growth of the cyclopoid copepod *Oithona nana*. *Diversity*, *13*, 190–199.

Maier, C., Hegeman, J., & Weinbauer, M. G. (2009). Calcification of the cold-water coral *Lophelia pertusa* under ambient and reduced pH. *Biogeosciences*, *6*, 1671–1680.

Maier, C., Popp, P., Sollfrank, N., Weinbauer, M. G., Wild, C., & Gattuso, J.-P. (2016). Effects of elevated pCO_2 and feeding on net calcification and energy budget of the Mediterranean cold-water coral *Madrepora oculata*. *Journal of Experimental Biology*, *219*(20), 3208–3217. https://doi.org/10.1242/jeb.127159

Maier, S. R., Bannister, R. J., Van Oevelen, D., & Kutti, T. (2020). Seasonal controls on the diet, metabolic activity, tissue reserves and growth of the cold-water coral Lophelia pertusa. *Coral Reefs*, *39*(1), 173–187. https://doi.org/10.1007/s00338-019-01886-6

Maier, S. R., Jantzen, C., Laudien, J., Häussermann, V., Försterra, G., Niggemann, J., Dittmar, T., & Richter, C. (2021). The carbon and nitrogen budget of *Desmophyllum dianthus*—A voracious cold-water coral thriving in an acidified Patagonian fjord. *PeerJ*, *9*(9), e12609.

Maier, S. R., Kutti, T., Bannister, R. J., Breugel, P., Rijswijk, P., & Oevelen, D. (2019). Survival under conditions of variable food availability: Resource utilization and storage in the cold-water coral *Lophelia pertusa*. *Limnology and Oceanography*, *64*(4), 1651–1671. https://doi.org/10.1002/lno.11142

Maldonado, M., Aguilar, R., Bannister, R. J., Bell, J. J., Conway, K. W., Dayton, P. K., Díaz, C., Gutt, J., Kelly, M., Kenchington, E. L. R., Leys, S. P., Pomponi, S. A., Rapp, H. T., Rützler, K., Tendal, O. S., Vacelet, J., & Young, C. M. (2015). Sponge grounds as key marine habitats: A synthetic review of types, structure, functional roles, and conservation concerns. In S. Rossi, L. Bramanti, A. Gori, & C. Orejas Saco del Valle (Eds.), *Marine animal forests* (pp. 1–39). Springer International Publishing. https://doi.org/10.1007/978-3-319-17001-5_24-1

Martínez-Alarcón, D., Saborowski, R., Melis, E., & Hagen, W. (2019). Seasonal lipid dynamics of the shrimps *Crangon crangon* and *Pandalus montagui* in the German Bight (North Sea). *Marine Ecology Progress Series*, *625*, 41–52. https://doi.org/10.3354/meps13046

Mezek, T., Simčič, T., Arts, M. T., & Brancelj, A. (2010). Effect of fasting on hypogean (*Niphargus stygius*) and epigean (*Gammarus fossarum*) amphipods: A laboratory study. *Aquatic Ecology*, *44*(2), 397–408. https://doi.org/10.1007/s10452-009-9299-7

Meziane, T., & Tsuchiya, M. (2000). Fatty acids as tracers of organic matter in the sediment and food web of a mangrove/intertidal flat ecosystem, Okinawa, Japan. *Marine Ecology Progress Series*, *200*, 49–57. https://doi.org/10.3354/meps200049

Monroig, Ó., & Kabeya, N. (2018). Desaturases and elongases involved in polyunsaturated fatty acid biosynthesis in aquatic invertebrates: A comprehensive review. *Fisheries Science*, *84*(6), 911–928. https://doi.org/10.1007/s12562-018-1254-x

Montero, P. M., Daneri, G., Tapia, F., Iriarte, J. L., & Crawford, D. (2017). Diatom blooms and primary production in a channel ecosystem of Central Patagonia. *Latin American Journal of Aquatic Research*, *45*(5), 999–1016. https://doi.org/10.3856/vol45-issue5-fulltext-16

Mueller, C. E., Larsson, A. I., Veuger, B., Middelburg, J. J., & van Oevelen, D. (2014). Opportunistic feeding on various organic food sources by the cold-water coral *Lophelia pertusa*. *Biogeosciences*, *11*(1), 123–133. https://doi.org/10.5194/bg-11-123-2014

Naumann, M. S., Orejas, C., Wild, C., & Ferrier-Pagès, C. (2011). First evidence for zooplankton feeding sustaining key physiological processes in a scleractinian cold-water coral. *Journal of Experimental Biology*, *214*(21), 3570–3576. https://doi.org/10.1242/jeb.061390

Naumann, M. S., Tolosa, I., Taviani, M., Grover, R., & Ferrier-Pagès, C. (2015). Trophic ecology of two cold-water coral species from the Mediterranean Sea revealed by lipid biomarkers and compound-specific isotope analyses. *Coral Reefs*, *34*(4), 1165–1175. https://doi.org/10.1007/s00338-015-1325-8

Orejas, C., Gili, J., López-González, P., & Arntz, W. (2001). Feeding strategies and diet composition of four Antarctic cnidarian species. *Polar Biology*, *24*(8), 620–627. https://doi.org/10.1007/s003000100272

Orejas, C., Gori, A., Rad-Menéndez, C., Last, K. S., Davies, A. J., Beveridge, C. M., Sadd, D., Kiriakoulakis, K., Witte, U., & Roberts, J. M. (2016). The effect of flow speed and food size on the capture efficiency and feeding behaviour of the cold-water coral *Lophelia pertusa*. *Journal of Experimental Marine Biology and Ecology*, *481*, 34–40. https://doi.org/10.1016/j.jembe.2016.04.002

R Core Team. (2020). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Radice, V. Z., Brett, M. T., Fry, B., Fox, M. D., Hoegh-Guldberg, O., & Dove, S. G. (2019). Evaluating coral trophic strategies using fatty acid composition and indices. *PLoS One*, *14*(9), e0222327. https://doi.org/10.1371/journal.pone.0222327

Rakka, M., Maier, S. R., Van Oevelen, D., Godinho, A., Bilan, M., Orejas, C., & Carreiro-Silva, M. (2021). Contrasting metabolic strategies of two co-occurring deep-sea octocorals. *Scientific Reports*, *11*(1), 10633. https://doi.org/10.1038/s41598-021-90134-5

Roberts, J. M., Wheeler, A. J., & Freiwald, A. (2006). Reefs of the deep: The biology and geology of cold-water coral ecosystems. *Science*, *312*(5773), 543–547. https://doi.org/10.1126/science.1119861

Rocker, M. M., Francis, D. S., Fabricius, K. E., Willis, B. L., & Bay, L. K. (2019). Temporal and spatial variation in fatty acid composition in *Acropora tenuis* corals along water quality gradients on the great barrier reef, Australia. *Coral Reefs*, *38*(2), 215–228. https://doi.org/10.1007/s00338-019-01768-x

Rogers, A. D. (1999). The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep-water reef-forming corals and impacts from human activities. *International Review of Hydrobiology*, *84*(4), 315–406. https://doi.org/10.1002/iroh.199900032

Rossi, S., Bramanti, L., Gori, A., & Orejas, C. (2017). Animal forests of the world: An overview. In S. Rossi, L. Bramanti, A. Gori, & C. Orejas (Eds.), *Marine animal forests: The ecology of benthic biodiversity*

hotspots (pp. 1–28). Springer International Publishing. https://doi.org/10.1007/978-3-319-21012-4_1

RStudio Team. (2020). *RStudio: Integrated development environment for R*. RStudio, PBC http://www.rstudio.com/

Russo, G. L. (2009). Dietary n−6 and n−3 polyunsaturated fatty acids: From biochemistry to clinical implications in cardiovascular prevention. *Biochemical Pharmacology*, *77*(6), 937–946. https://doi.org/10.1016/j.bcp.2008.10.020

Sánchez, N., González, H. E., & Iriarte, J. L. (2011). Trophic interactions of pelagic crustaceans in Comau Fjord (Chile): Their role in the food web structure. *Journal of Plankton Research*, *33*(8), 1212–1229. https://doi.org/10.1093/plankt/fbr022

Sargent, J., Bell, J. G., Bell, M. V., Henderson, R. J., & Tocher, D. R. (1993). The metabolism of phospholipids and polyunsaturated fatty acids in fish. In *Aquaculture: Fundamental and applied research* (pp. 103–124). American Geophysical Union (AGU). https://doi.org/10.1029/CE043p0103

Sargent, J., & Falk-Petersen, S. (1988). The lipid biochemistry of calanoid copepods. *Hydrobiologia*, *167/168101-114*, 101–114.

Sargent, J., & Whittle, K. J. (1981). *Lipids and hydrocarbons in the marine food web*. Analysis of Marine Ecosystems/A. R.

Schaafsma, F. L., Cherel, Y., Flores, H., van Franeker, J. A., Lea, M.-A., Raymond, B., & van de Putte, A. P. (2018). Review: The energetic value of zooplankton and nekton species of the Southern Ocean. *Marine Biology*, *165*(8), 129. https://doi.org/10.1007/s00227-018-3386-z

Schlechtriem, C., Arts, M. T., & Johannsson, O. E. (2008). Effect of long-term fasting on the use of fatty acids as trophic markers in the opossum shrimp *Mysis relicta*—A laboratory study. *Journal of Great Lakes Research*, *34*(1), 143–152. https://doi.org/10.3394/0380-1330(2008)34[143:EOLFOT]2.0.CO;2

Schlichter, D., Zscharnack, B., & Krisch, H. (1995). Transfer of photoassimilates from endolithic algae to coral tissue. *Naturwissenschaften*, *82*(12), 561–564. https://doi.org/10.1007/BF01140246

Schlitzer, R. (2021). *Ocean data* view. https://odv.awi.de

Scott, C., Kwasniewski, S., Falk-Petersen, S., & Sargent, J. (2002). Species differences, origins and functions of fatty alcohols and fatty acids in the wax esters and phospholipids of *Calanus hyperboreus*, *C. glacialis* and *C. finmarchicus* from Arctic waters. *Marine Ecology Progress Series*, *235*, 127–134. https://doi.org/10.3354/meps235127

Sebens, K. P. (1982). The limits to indeterminate growth: An optimal size model applied to passive suspension feeders. *Ecology*, *63*(1), 209–222. https://doi.org/10.2307/1937045

Siegfried, C. A., & Kopache, M. E. (1980). Feeding of *Neomysis mercedis* (Holmes). *The Biological Bulletin*, *159*(1), 193–205. https://doi.org/10.2307/1541018

Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional Ecology*, *3*(3), 259. https://doi.org/10.2307/2389364

Sweetman, A. K., Thurber, A. R., Smith, C. R., Levin, L. A., Mora, C., Wei, C.-L., Gooday, A. J., Jones, D. O. B., Rex, M., Yasuhara, M., Ingels, J., Ruhl, H. A., Frieder, C. A., Danovaro, R., Würzberg, L., Baco, A., Grupe, B. M., Pasulka, A., Meyer, K. S., … Roberts, J. M. (2017). Major impacts of climate change on deep-sea benthic ecosystems. *Elementa: Science of the Anthropocene*, *5*, 4. https://doi.org/10.1525/elementa.203

Tocher, D. R. (2003). Metabolism and functions of lipids and fatty acids in teleost fish. *Reviews in Fisheries Science*, *11*(2), 107–184. https://doi.org/10.1080/713610925

van Oevelen, D., Duineveld, G. C. A., Lavaleye, M. S. S., Kutti, T., & Soetaert, K. (2018). Trophic structure of cold-water coral communities revealed from the analysis of tissue isotopes and fatty acid composition. *Marine Biology Research*, *14*(3), 287–306. https://doi.org/10.1080/17451000.2017.1398404

Wall, M., Beck, K. K., Garcia-Herrera, N., Schmidt-Grieb, G. M., Laudien, J., Höfer, J., Försterra, G., Held, C., Nehrke, G., Espinoza, J. P., Woll, M., Graeve, M., & Richter, C. (2023a). Data from: Physical oceanographic profiles of seven CTD casts from Gulf of Ancud into Comau Fjord in 2016. PANGAEA https://doi.org/10.1594/PANGAEA.962593

Wall, M., Beck, K. K., Garcia-Herrera, N., Schmidt-Grieb, G. M., Laudien, J., Höfer, J., Försterra, G., Held, C., Nehrke, G., Espinoza, J. P., Woll, M., Graeve, M., & Richter, C. (2023b). Data from: *Desmophyllum dianthus* relative and absolute fatty acid and fatty alcohol composition in Comau Fjord, Chile. PANGAEA https://doi.org/10.1594/PANGAEA.962841

Wells, S. R., Bresnan, E., Cook, K., Eerkes-Medrano, D., Machairopoulou, M., Mayor, D. J., Rabe, B., & Wright, P. J. (2021). Environmental drivers of a decline in a coastal zooplankton community. *ICES Journal of Marine Science*, *79*(3), 844–854.

Wiborg, K. F. (1954). *Investigations on zooplankton in coastal and offshore waters of western and northwestern Norway—With special reference to the copepods*. (report on Norwegian Fishery and Marine Investigations, p. 244).

Yamashiro, H., Oku, H., & Onaga, K. (2005). Effect of bleaching on lipid content and composition of Okinawan corals. *Fisheries Science*, *71*(2), 448–453. https://doi.org/10.1111/j.1444-2906.2005.00983.x

Yasuda, T., Oda, M., Tanaka, S., Nanjo, N., Takahashi, M., & Fukuwaka, M. (2021). Selective retention and transfer of long-chain polyunsaturated fatty acids in Japanese sardine. *Marine Biology*, *168*(12), 172. https://doi.org/10.1007/s00227-021-03985-x

Yen, J. (1985). Selective predation by the carnivorous marine copepod *Euchaeta elongata*: Laboratory measurements of predation rates verified by field observations of temporal and spatial feeding patterns. *Limnology and Oceanography*, *30*(3), 577–597. https://doi.org/10.4319/lo.1985.30.3.0577

DATA SOURCES

Beck, K., Schmidt-Grieb, G., Laudien, J., Försterra, G., Häussermannn, V., González, H., Espinoza, J., Richter, C., & Wall, M. (2022). Environmental stability and phenotypic plasticity benefit the cold-water coral *Desmophyllum dianthus* in an acidified fjord. *Communications Biology*, *5*(1), 683. in press.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Comparison of the biochemical composition with other *Desmophyllum* and cold-water coral species.

Figure S1. Fatty acid biosynthesis pathways.

Figure S2. Average environmental conditions during sampling.

Figure S3. Heatmaps of fatty acid and fatty alcohol composition of individual corals.

Figure S4. Fatty acid ratios as putative health indicators.

Table S1. List of fatty acids (FAs) as well fatty alcohols.

How to cite this article: Wall, M., Beck, K. K., Garcia-Herrera, N., Schmidt-Grieb, G. M., Laudien, J., Höfer, J., Försterra, G., Held, C., Nehrke, G., Espinoza, J. P., Woll, M., Graeve, M., & Richter, C. (2023). Lipid biomarkers reveal trophic relationships and energetic trade-offs in contrasting phenotypes of the cold-water coral *Desmophyllum dianthus* in Comau Fjord, Chile. *Functional Ecology*, *00*, 1–17. https://doi.org/10.1111/1365-2435.14479